University of Alberta

Effects of grazing on vegetation dynamics in Australian White Box woodland

by

Kimberly Gail Allcock

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Doctor of Philosophy

in

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27 September 2002

Dedication

To my father, Barry Arthur Allcock. You were always interested and believed I could do anything. I wish you could be here in person, but I know you're here in spirit and are as proud as you can be. I miss you.

Abstract

Grazing affects plant community composition, sometimes creating irreversible changes in vegetation and soils. This may be evident in disturbed and fragmented ecosystems such as White Box (*Eucalyptus albens*) woodlands in southeastern Australia. I investigated the effects of herbivory by kangaroos, sheep, cattle, and rabbits on white box woodland vegetation, and identified potential asymmetric boundaries associated with vegetation change.

I monitored vegetation and soils in a four-year herbivore exclusion experiment at Burrendong Dam NSW, planted native seedlings in experimental plots and monitored their growth and survival, conducted a controlled greenhouse experiment to measure growth and competition of native and exotic species, and surveyed vegetation and soils in regional woodland remnants.

Herbivory influenced soils, seedling survival and growth, and species composition. Exclusion of stock and kangaroos resulted in the largest changes, including improvement of soil nutrient cycling and an increase in native grasses. However, species typical of less-disturbed woodland did not appear inside exclosures over the course of the study. Differences in the responses of native seedlings to exclusion of different herbivores indicated that management of particular herbivores could shift species composition. Native species richness declined and exotic richness increased with increasing biomass. In addition, exotic species showed greater growth and competitive effects than native species under phosphorus enrichment.

In the context of a state and transition model, my results suggest two asymmetric boundaries: one related to loss of native species, the other to exotic species invasion and

soil nutrients. Reduction of herbivory does not appear to allow reverse shifts across boundaries without other intervention, at least in the short term. Herbivore control will be an essential step in managing and restoring remnant white box woodlands, but stock reduction alone will not be effective, and even if all herbivores are excluded further intervention will be required.

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Chapter 1

General Introduction

Herbivory in plant communities

Herbivory can be a major structuring force in plant communities, affecting plants directly by consuming biomass or individuals, or indirectly by modifying soils and species interactions (McNaughton 1979, 1983, Crawley 1986, Huntley 1991, Hulme 1996, Ritchie and Olff 1999, Ryerson and Parminter 2001). Vegetation responses are widely variable. The effects of herbivores in grassy ecosystems may be especially important because such systems are often space and light limited (e.g. Collins *et al.* 1998) and because many such ecosystems are currently utilized for domestic stock production (e.g. Noy-Meir *et al.* 1989, Pettit *et al.* 1995, Walker *et al.* 1997, Perevolotsky and Seligman 1998, Stohlgren *et al.* 1999, Austerheim and Eriksson 2001). In ecosystems with a variety of herbivore species, the response of vegetation to herbivory can be further complicated by differences in feeding mode, behavior, and preferences (Huntley 1991, Hulme 1996, Ritchie and Olff 1999) resulting in both additive or compensatory effects of multiple herbivore species.

Herbivory acts as a disturbance in plant communities (Connell and Slatyer 1977, Sousa 1984, Huntley 1991), initiating vegetation change by creating gaps for recruitment (small-scale secondary succession – Connell and Slatyer 1977). This may result in increased species diversity by increasing heterogeneity and producing recruitment microsites, or by reducing the dominance of strongly competitive species (Denslow 1985). Selective herbivory can cause both elimination of palatable species, or reduced competition by dominant species thus either decreasing or increasing diversity (Crawley

1986, Huntley 1991). Herbivores can also contribute to spatial patterns within plant communities, generally increasing heterogeneity (Steinauer and Collins 2001, Adler *et al.* 2001). At the population level, plant modules (leaves, rametes, shoots) tend to be more strongly affected than entire genetes except at the seedling stage; however changes in longevity, flowering, and growth form are likely and these can lead to changes in community composition (Crawley 1986).

The effects of herbivory can interact with productivity to produce a wide range of results, including both acceleration and slowing of succession (e.g. Tilman 1988, Fraser and Grime 1999, Van der Wal *et al.* 2000) or alteration of native and exotic species diversity (Safford and Harrison 2001). Herbivory in productive environments may increase diversity while in less productive environments it may reduce diversity (Huston 1979). In addition, vegetation change in response to changes in herbivory may be more pronounced in productive habitats (Milchunas and Lauenroth 1993, Proulx and Mazumder 1998).

Herbivores, in particular large mammalian herbivores, can also substantially influence nutrient cycling and soil properties (though the changes are not always consistent in direction; Milchunas and Lauenroth 1993). There is substantial evidence that herbivores can increase the rate of nutrient cycling (particularly nitrogen) and create nutrient feedbacks that may alter spatial structure of vegetation (e.g. Wedin 1999, Herrick and Whitford 1999, Steinauer and Collins 2001). In Australian ecosystems, the introduction of hard-footed grazing animals (sheep and cattle) has caused compaction and erosion of soils, destruction of cryptobiotic crusts, and changes in nutrient distribution (Tonkinson and Costello 1994). There is also evidence that herbivory can alter root biomass, below-

ground competition, and even mycorhizzal associations of plant species (Crawely 1986, Eom *et al.* 2001).

Multiple states in grazing systems

Vegetation changes in response to grazing disturbance have often been treated as secondary succession (*sensu* Clements 1916: Smith 1989, Milchunas and Lauenroth 1993, Vayssieres and Plant 1998). The standard model for assessing condition of rangeland ecosystems, the "range condition" (RC) model (Dykerstuis 1949) assumes that rangeland vegetation undergoes a series of predictable and reversible compositional changes with changes in grazing pressure (e.g. Pendleton 1989). However, herbivory can create seemingly irreversible changes in vegetation composition and soils, resulting in more than one stable vegetation state (eg. Noy-Meier 1975, Dublin *et al.* 1990, Laycock 1991, Hik *et al.* 1992, Bellamy and Brown 1994, Hodgekinson and Cook 1995, Brejda 1997, Augustine *et al.* 1998).

It is now generally agreed that rangeland dynamics under grazing often do not meet the assumptions of a secondary-succession-based range condition model (e.g. Smith 1989) and more complicated views of vegetation change (for example, the state and transition model -Westoby *et al.* 1989a,b) have come to replace the range condition model in management of rangelands (Vayssieres and Plant 1998, Scarnecchia 1995, Smith *et al.* 1995, Stringham 2001). The state and transition (S&T) model describes vegetation dynamics in terms of a set of discrete 'states' that can occur on a particular site, and 'transitions' between these states that can be triggered by natural events (fire, weather) or management actions (change in stocking rate, fertilization) (Westoby *et al.* 1989a). The

S&T model is based on discrete states with boundaries and transitions between them, and degree of variation (possibly similar to the classical view of vegetation change with herbivory disturbance) is possible within each of the states. This can be illustrated using a "ball and cup" diagram to depict multiple state dynamics (Holling 1973; Figure 1.1). Mild disturbance can move the "ball" around within a particular basin, allowing for a return to the original state with cessation of the disturbance, while a large enough disturbance can cause a dramatic change in the community, shifting the "ball" from one basin to another.

State and transition models have some shortcomings, including subjectivity and difficulty of testing (Rodreguez Iglesias and Kothman 1997, Allen-Diaz and Bartelome 1998). However, they are being effectively applied in management of rangeland and other habitats (e.g. Vayssieres and Plant 1998, Tugel and Brown 2001, Stringham *et al.* 2001). Thinking about vegetation change in the context of state and transition models allows for the identification of asymmetric boundaries and thresholds between vegetation states. This could prove especially advantageous when attempting to understand discontinuous vegetation change in fragmented or highly modified ecosystems.

Australian woodlands: Description, Status, and Conservation

Temperate eucalypt woodlands (defined as treed habitats with trees providing up to 30% foliar cover) were once widespread across the agricultural zones of Australia (Yates and Hobbs 2000), occurring on relatively fertile soils in areas receiving between 400 and 900 mm rainfall annually (Benson 1999). They likely existed within a mosaic landscape of treeless valleys, timbered slopes, and other habitats (Benson and Redpath 1997, Yates

and Hobbs 2000), but were much more widespread than presently. There is some controversy over the processes creating these savanna ecosystems, but it appears that soils and topography, climate, light grazing, and patchy fire probably helped maintain the mosaic nature of the vegetation (Benson and Redpath 1997).

Temperate woodlands were rapidly converted to agricultural uses after European settlement, resulting in present-day ecosystems that are much fragemented and modified (Benson 1991, Prober and Thiele 1993, 1995, Yates and Hobbs 1997a, 2000). There has been widespread loss of species and degradation of soil (e.g. Yates and Hobbs 1997b, Sivertsen and Clarke 2000, Bauer and Goldney 2000), and threats such as weed invasion, tree clearing, and grazing by feral and domestic animals continue (e.g. Sivertsen and Clarke 2000, and many other examples in that volume).

White Box (*Eucalyptus albens*) woodlands in the central west slopes region of New South Wales have been severely degraded since European settlement in the early 19th century. The pre-European understory vegetation is not well known, but it likely consisted of a predominantly grassy understory composed primarily of *Themeda australis* (kangaroo grass) and *Poa sieberiana* (snow tussock) with a limited shrub layer, numerous sub-dominant grass species (including spear grasses *Austrostipa spp.* and wallaby grasses *Austrodanthonia spp.*), and many annual and perennial forbs growing between grass tussocks (Prober and Thiele 1993, 1995, Windsor 2000). Today, as much as 90% of the original box woodlands have been cleared (Benson 1991), and an estimated 0.01% of White Box woodlands remain relatively unmodified (Prober and Thiele 1993). Once a continuous belt of vegetation stretching the length of New South Wales, the woodlands

now consist of small remnants in varying degrees of decline surrounded by exotic pasture and crop land. Figure 1.2 illustrates some species typical of woodland remnants.

Programs to encourage conservation and restoration of remnant bushland include reducing stocking rates, controlling exotic plant species, planting trees (Nowland 1997, Barlow 1998), or supplying subsidies for stock fencing and tree planting (e.g. Elix and Lambert 1997, Lambert *et al.* 2000, Spooner 2002). However, stock grazing is only one of several processes contributing to degradation of box woodlands (Yates and Hobbs 1997a, Sivertsen and Clarke 2000), and at least 42% of remnant patches in central western NSW are so degraded that they cannot be sustained without additional intervention (Goldney *et al* 1995). The fragmented nature of remnant box woodlands creates a further management challenge, and will require both an administrative infrastructure capable of dealing with spatially disjunct areas (e.g. Thiele and Prober 2000, Prober *et al.* 2001) and a good understanding of vegetation dynamics in fragmented and degraded remnants.

Research Objectives

I had two primary objectives for this study: 1. to understand the effects of herbivory by kangaroos, sheep, cattle, and rabbits on vegetation in white box woodland with a history of human disturbance; and 2. to use a state and transition framework to identify potential thresholds to vegetation change and to subsequently test these either experimentally or by comparing historical and regional data on soils, management history, and vegetation composition. Grazing is currently the primary disturbance structuring vegetation in white box woodland, and manipulating this disturbance allowed

some predictions of diversity theory to be tested. In addition, herbivore management (usually de-stocking or rabbit control) is often used as a means to restore degraded woodland remnants, though the impacts of the different herbivore species are not known. Finally, habitat fragmentation and past management may have created boundaries to vegetation change even with herbivore exclusion.

Study Site and Regional History

The main study area used for this research was part of a large catchment managed by the Department of Land and Water Conservation, New South Wales (Figure 1.3). It was located on the foreshores of Lake Burrendong (32° 40' S, 149° 6' E) at the confluence of the Macquarie and Cudgegong Rivers on the western slopes of the Great Dividing Range in eastern Australia. The lake is a large reservoir used for flood mitigation, irrigation, and recreation, and was created in 1967 with the completion of Burrendong Dam. The climate of the region is temperate, with warm summers (mean max. 29-33θ C), cool winters (mean min. 2-3θC), and an annual rainfall of 666±29 mm yr^{-1} (mean±SE, 1951-1998 rainfall, Australian Bureau of Meteorology, Site No. 062003 - Mumbil).

The central west slopes and tablelands were among the earliest inland areas settled by Europeans, with the towns of Bathurst (approximately 200km south of the Burrendong site) established in 1813 and Wellington (just west of the Burrendong site) in 1823 (Clarke 1993). The region north of Bathurst was first surveyed in the early 1820s by Sir Thomas Mitchell, (surveyor's notebooks, 1822). His sketches of the area show a mosaic landscape of woodlands and plains with rocky outcrops covered in native conifers and stringybark eucalypts including *Eucalyptus macrorhynchos*. East of the Cudgegong the

landscape consisted of limestone hills, cypress pine dominated ridges, and grassy fertile vales. Towards the Macquarie the land is described as well timbered ranges rising progressively in elevation from the fertile flats of the river. North of Wellington, he noted a "flatland depressed country in the distance" (this is probably the pilliga scrub, near Dubbo). In general historic descriptions provide an impression of a patchy landscape: rolling hills, fertile valleys, rocky ridges with stringybark and cypress pine, granite outcrops with scrub, grazing land, and both wooded and grassy hills.

The long history of European settlement in the region, along with the generally fertile nature of the native grasslands and grassy box woodlands resulted in substantial modification of the original vegetation. Changes to the box woodlands due to livestock grazing, clearing and decreased fire frequency rapidly followed settlement. Invasion by annual exotic grasses (*Briza minor*, *Bromus* spp., *Vulpia* spp., and *Hordeum* spp.) was evident in 1878 (Bentham 1878). Because temperate woodlands tended to occur on better quality soils, most of the woodlands were rapidly cleared for cropping or modified by livestock grazing leaving a patchwork of remnants (Bowie and Goldney 1987, Benson 1991, Lunt 1991, Prober and Thiele 1993, 1995, McDougall and Kirkpatrick 1994, Prober *et al.* 2001).

At the Burrendong site, the oldest settlement leases were dated 1885. Because of the Australian Gold Rush much of the Burrendong area was reserved from conditional sale to maintain mining rights. The Wellington Gold Fields were proclaimed in 1861 and notified and reserved in 1878. Grazing and residential leases on reserved gold field territory came during and after WW1 (1912-1920). The portions of the Lake Burrendong foreshores that were used in our experiments were generally owned and managed by

approximately 12 different landholders at any one time. Many of these properties are now below the high water mark for the dam, especially those properties that were not part of the reserved land for the Wellington gold field.

The typical conditions for homestead or paddock improvement leases often involved considerable modifications to the land. Homestead selections required creation and maintenance of drainage channels, provision of watering points, preservation or planting of shade and timber trees but ring-barking of other trees, and mineral rights were usually reserved. Often rabbit and prickly pear control were an additional conditions. The following quote cites the conditions for a lease near Dubbo (a property named "Merebone", lease application dated 1895):

> "To be kept entirely free of Rabbits or other noxious animals. At least 2/3 of growing timber to be ring-barked, retaining where possible sufficient provision for shade or fire break. Provision to be made for an ample water supply. To be kept entirely free of undergrowth, noxious weeds, and scrub, and Prickly Pear".

Many other leases contained stipulations to clear scrub and understory, to keep ring-barked land clear of suckers and regeneration, and sometimes to retain timber stands (cypress pine and ironbark).

Leaseholders at Burrendong were notified in 1945 that their land would be expropriated for the creation of Burrendong Dam. Expropriation took place from 1949-1951, though some patches were appropriated as late as 1961. In December 1951, a portion of the Burrendong study area was declared a Fauna Protection Area but this was

limited primarily to the poor grazing land (steep scrubby ridges and cypress pine dominated slopes).

When the foreshore land was reclaimed much of it was in poor condition, with large expanses of noxious weeds, little perennial cover, and widespread sheet erosion (McCaffrey 1951, Colclough 1960). The Soil Conservation Service of New South Wales undertook major restoration efforts in the 1960s, including de-stocking (both sheep and cattle), rabbit control, and seeding of clover (Logan 1957 a,b, Colclough 1960). They successfully re-established substantial perennial cover, controlled weeds, and in some cases encouraged dense tree regeneration. The resulting landscape at Burrendong (Figure 1.4) is a mosaic of steep heavily timbered slopes, rolling grasslands (cleared woodlands) with mixed native and exotic composition, remnant patches of white box woodland with modified understory, and heavily utilized, highly productive drainage lines with alluvial soils.

Remnant woodland patches at Burrendong typically have an overstory of white box, a limited shrub layer consisting primarily of *Olearia elliptica* (sticky daisy-bush), and *Dodonea viscosa* (hop-bush), grassy ground layer vegetation dominated by *Bothriochloa macra* (which occurs mostly in canopy gaps) and other perennial grasses such as *Austrostipa scabra*, *Austrodanthonia racemosa* and *Microlaena stipoides*. Occasional small patches of *Poa sieberiana* and *Themeda australis* are still present but these species are never dominant. Exotic species, mostly annual forbs and grasses, can be abundant especially in winter and spring. In grassland patches (where the overstory was removed for pasture improvement) the ground layer is similar, but has a higher abundance of exotic species, especially exotic annual grasses such as *Vulpia* and *Bromus* spp. In

alluvial drainages exotic annual species (notably *Echium plantagineum*) can be dominant, especially in areas heavily used by stock.

Experimental Design

In February 1997, we established the central grazing experiment for this study. This consisted of a series of fences to investigate the response of woodland, grassland, and alluvial habitats to exclusion of herbivory and to test for differences between the effects of different herbivores. The experiment was replicated in four blocks across the Burrendong study area, with each block a creek watershed (Figure 1.5). Within each block, there were twelve 25m by 25m experimental plots, distributed evenly in woodland (intact canopy), grassland (canopy cleared), and alluvial drainages. In some cases the alluvial drainages were too narrow to accommodate a square plot, so rectangular plots measuring 16.5m by 33m were established instead. Each plot was subjected to one of four treatments: control (no fence) stock fence (to exclude domestic sheep and cattle), kangaroo fence (to exclude macropods and stock), and complete exclosure (to exclude rabbits, macropods, and stock), for a total of 48 plots (four replicates of each habitat/fence combination. See figures 1.6 and 1.7).

Thesis organization

This study was designed to investigate the response of vegetation to herbivore management, to determine whether exclusion of different species of herbivores resulted in different vegetation responses over four years, and to identify asymmetric boundaries to vegetation change in white box woodland remnants. Most of the chapters presented

here deal with research conducted within the context of the herbivore exclusion experiment described above (Chapters 2, 4, and 5). Additional experiments and surveys of other white box remnants in the region were used to gain information about potential asymmetric boundaries (Chapters 3 and 6).

This thesis consists of seven chapters, including the general introduction (Chapter 1) and a short concluding chapter (Chapter 7), and three appendices, two presenting lists of plant species recorded at Burrendong and in regional surveys, and a third describing the methods of Landscape Function Analysis (Chapter 5). Chapters 2-5 present original research (the results of the experimental components of this study). Chapter 6 uses a state and transition framework to synthesize our understanding of white box woodland vegetation dynamics at Burrendong, and is based on literature review, the results presented in Chapters 2-5, vegetation and soil surveys of remnants in the Burrendong region, and a summary of the M.Sc. research conducted by David Board (Board 2002). Chapters 2-6 are written for publication as individual manuscripts. The following paragraphs provide a brief introduction to each of these manuscripts.

Chapter 2: White box woodlands are subject to herbivory by a variety of mammals and each herbivore type may have a different effect on growth and survival of native seedlings. This experiment tested the effects of mammalian herbivores on the survival and growth of transplanted seedlings of two native trees (*Eucalyptus albens, Callitris glaucophylla),* and one native grass (*Themeda australis*) over 3 years. Seedlings were planted into grassland and woodland experimental plots from the herbivore exclusion experiment at Burrendong Dam (see *Experimental Design*), and survival and growth were

monitored from 1998 to 2001. A stage-based matrix model was used to predict the proportion of tree seedlings reaching 'escape height' (height at which damage by herbivores is minimal and the individual is likely to mature and reproduce) under different grazing regimes, and logistic regression was used to relate probability of flowering in *Themeda* to size and herbivore activity.

Chapter 3: There is evidence from Australian communities that phosphorus enrichment can facilitate invasion, and differential growth of native and exotic species under increased phosphorus is a possible mechanism. Two glasshouse experiments were designed to test the following three questions relating to species responses to phosphorus. 1. Do exotic and native species show different patterns of growth along a gradient of increasing phosphorus? 2. Do exotic species have a greater competitive effect on native species than do conspecifics? 3. Does phosphorus enrichment compound the competitive effect of exotic species on native species? Four native perennial species (*Themeda australis, Bothriochloa macra, Austrodanthonia racemosa* and *Eucalyptus albens*) and two exotic annual species (*Vulpia bromoides* and *Echium plantagineum*) were used. In the first experiment, plants were grown individually under six levels of soil phosphorus. In the second experiment, individuals of *Eucalyptus albens* and *B. macra* were grown alone, with a conspecific competitor, or with an exotic competitor under low or high phosphorus.

Chapter 4: Disturbance and standing crop are commonly related to species richness, and both these factors are affected by level of herbivory. In addition, native and exotic

species may respond differently to changes in both disturbance and standing crop, which is an important consideration when determining the best management actions for remnant woodlands. In this portion of the study the herbivore exclusion fences constructed at Burrendong Dam were used to investigate the relationships of disturbance, cover, and standing crop in to native, exotic, and total plant species richness at two spatial scales (1 m^2 and 625 m^2).

Chapter 5: This portion of the study used herbivore exclusion fences established at Burrendong Dam to investigate the effect of four years of herbivore exclusion on understory vegetation composition and soils. Vegetation cover and composition were monitored in spring and summer from 1997 to 2001, soil surface characteristics were assessed in 1999, and soil chemical parameters measured in 2001. Partial CCA and variation decomposition were used to determine whether grazing manipulation, habitat type, or soil parameters had the greatest influence on species composition. Comparisons of the responses of *a-priori* species groups were used to test whether there was a shift toward pre-European composition with grazing exclusion, and if so, which herbivores appeared to have the greatest influence. Finally, PCA and MANOVA were used to determine whether soil parameters differed among fencing treatments.

Chapter 6: Vegetation changes caused by herbivory cannot always be readily reversed by reducing or eliminating herbivore activity, and in such cases, asymmetric boundaries or thresholds exist between vegetation states. White box woodlands are highly fragmented and have been dramatically modified by grazing and other management. It is likely that

asymmetric boundaries exist in remnant white box woodlands, and these must be identified and overcome for conservation efforts to succeed. In this chapter a state and transition model based on literature review is proposed for white box woodlands. The results presented in Chapters 2-5, along with a survey of vegetation and soils in remnants surrounding Burrendong Dam and the results of research by Board (2002), are used to confirm and refine identified asymmetric boundaries.

General significance

Herbivory can be a major structuring force in vegetation communities, and the effects of several herbivore species on vegetation composition are complex and not well understood (Ritchie and Olff 1999). In addition, vegetation change following grazing disturbance is not always analogous to secondary succession and changes are not necessarily reversible by removing the disturbance. Boundaries to vegetation change are likely to be especially important in fragmented ecosystems and systems in which intense herbivory is a relatively recent occurrence. White box woodlands in New South Wales have been greatly modified and fragmented since European settlement, and there is considerable interest in conserving and restoring those that remain.

This study provided the opportunity to observe the response of vegetation to a variety of mammalian herbivores, to apply the concepts of multiple state theory to identify asymmetric boundaries (thresholds) in a fragmented ecosystem, and to use state and transition modelling to highlight restoration difficulties and opportunities for degraded remnant woodlands. Finally, the infrastructure and sampling protocols for monitoring of vegetation established in the course of this research will allow continued study of the

effects of herbivore exclusion on vegetation and soils in White Box woodlands in the long term.

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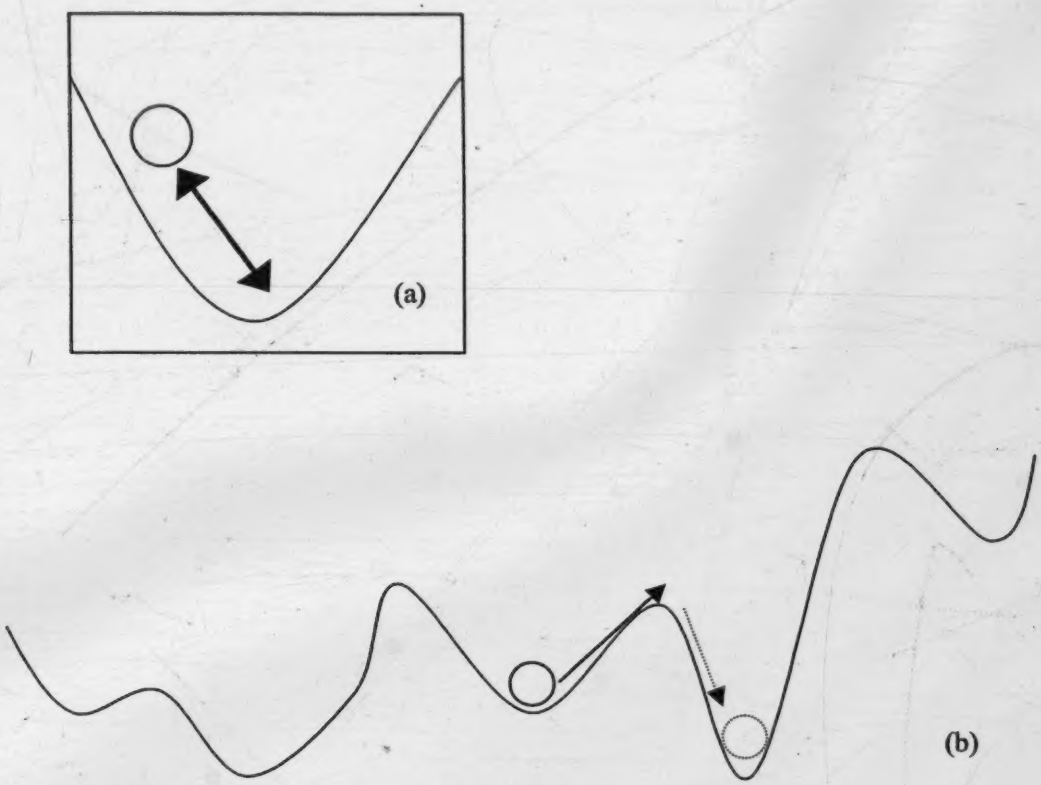

Figure 1.1: "Ball and cup" diagram used to represent the dynamics of an ecosystem that can exist in multiple stable states. The "cups" represent more or less stable configurations of the community (the "ball"), and the peaks between the cups represent boundaries between states that can be overcome by a large enough perturbation. Comparison of Figure 1(a) and 1(b) shows that traditional successional dynamics can be incorporated into a multiple state model: perturbations or disturbances that do not cause the system to cross a boundary create changes in composition that can be reversed by removing the disturbance, while shifts across boundaries are not reversible in this way.

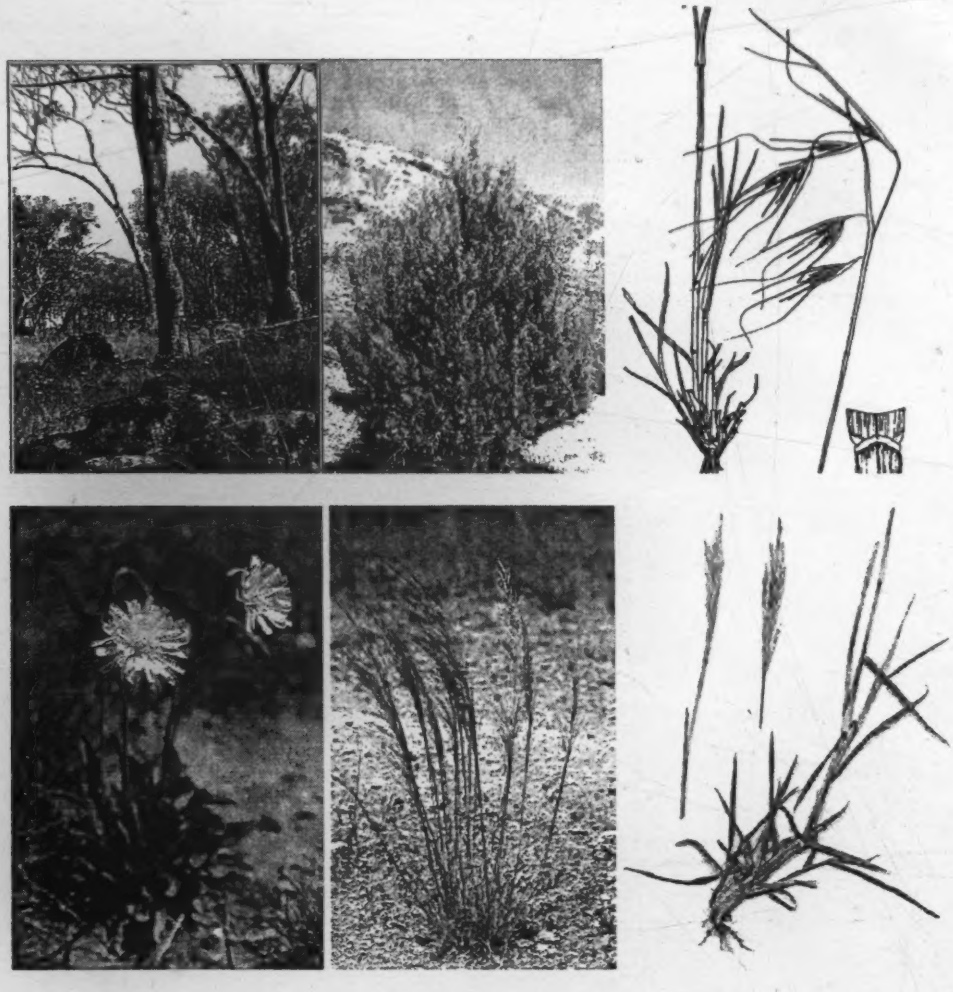

Figure 1.2: Species typical of white box woodland in New South Wales (l-r, top): *Eucalyptus albens* (photo K. Thiele), *Callitris glaucophylla* (photo Australian National Botanic Gardens: ANBG), *Themeda australis* (drawing Watson and Dallwitz 1999); (l-r, bottom): *Microseris lanceolata* (photo ANBG), *Austrostipa scabra* (photo ANBG), *Bothriochloa macra*. *Themeda* and *Microseris* are typical of less-disturbed woodlands; *Bothriochloa* and *Austrostipa* are common in areas with a history of stock grazing.

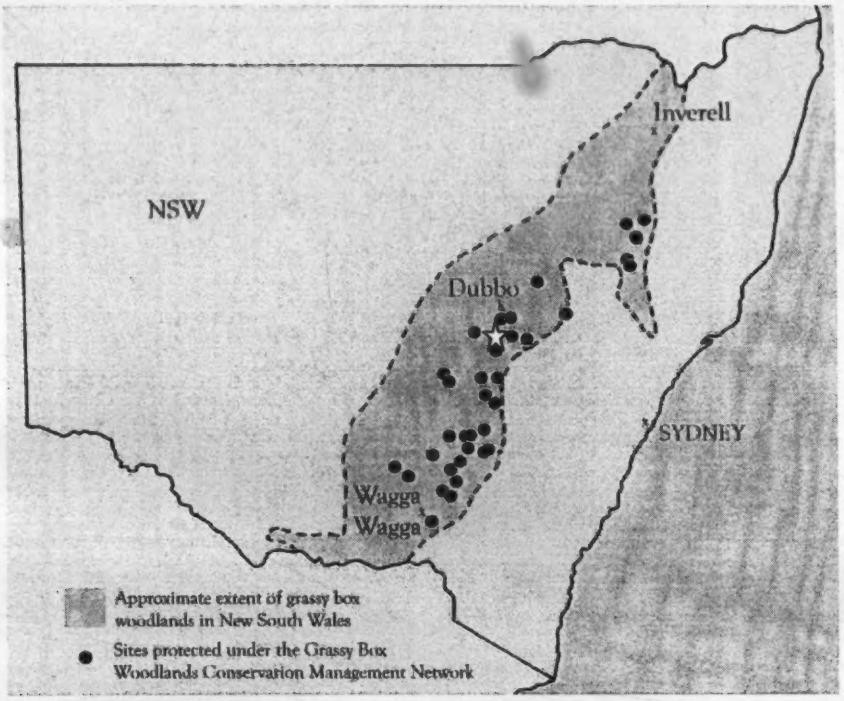

Figure 1.3: Distribution of remnant box woodlands in New South Wales (including white box, grey box, bimble box, poplar box, and yellow box). The dark grey area indicates the former distribution of box woodlands. Remnants indicated by dots have been included in the Conservation Management Network for box woodlands (Prober *et al.* 2001). The Burrendong Dam study area is indicated by a star. Map courtesy of Suzanne Prober.

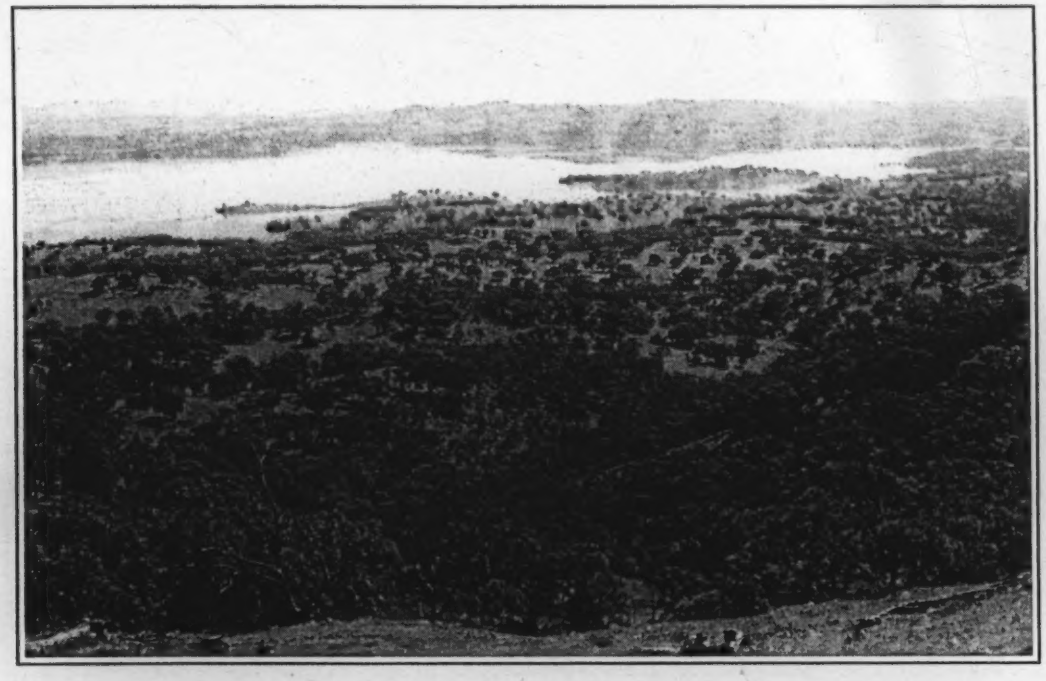

Figure 1.4: *Eucalyptus albens* woodland with patches of cleared pasture on the foreshores of Lake Burrendong, NSW.

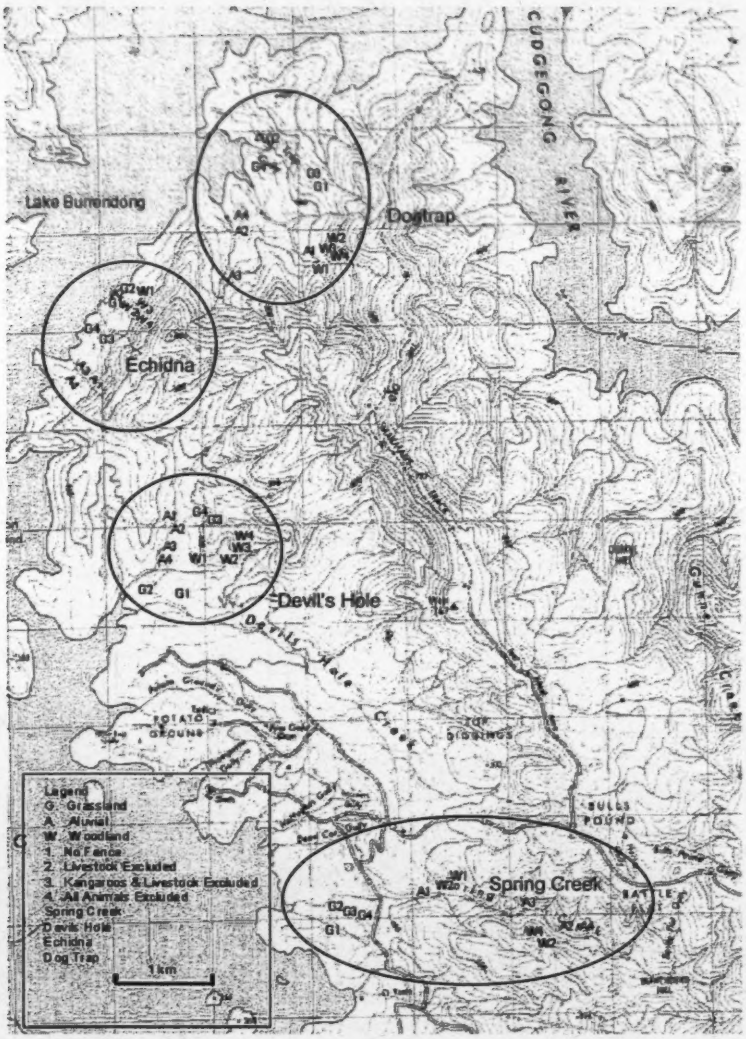

Figure 1.5: Distribution of experimental plots on the eastern foreshores of Burrendong Dam. "Dogtrap", "Echidna", "Devil's Hole" and "Spring Creek" are the names of the four creek watersheds used as blocks in the experimental design. Each watershed contained one replicate of each habitat/fencing treatment combination.

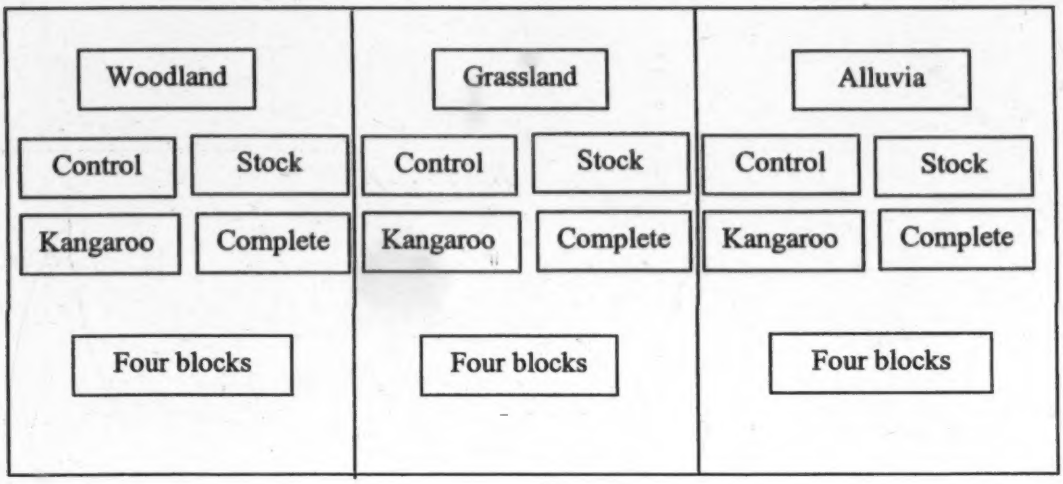

Figure 1.6: Diagrammatic representation of experimental design implemented at Burrendong Dam NSW. Experimental treatments were Control (unfenced), Stock exclusion (plainwire stock fence excluding sheep and cattle), Kangaroo exclusion (welded wire mesh fence excluding sheep, cattle, and kangaroos), and Complete exclosure (welded wire mesh with rabbit wire excluding sheep, cattle, kangaroos, and rabbits). These treatments were placed in three habitats, and replicated in four locations (see Figure 1.5).

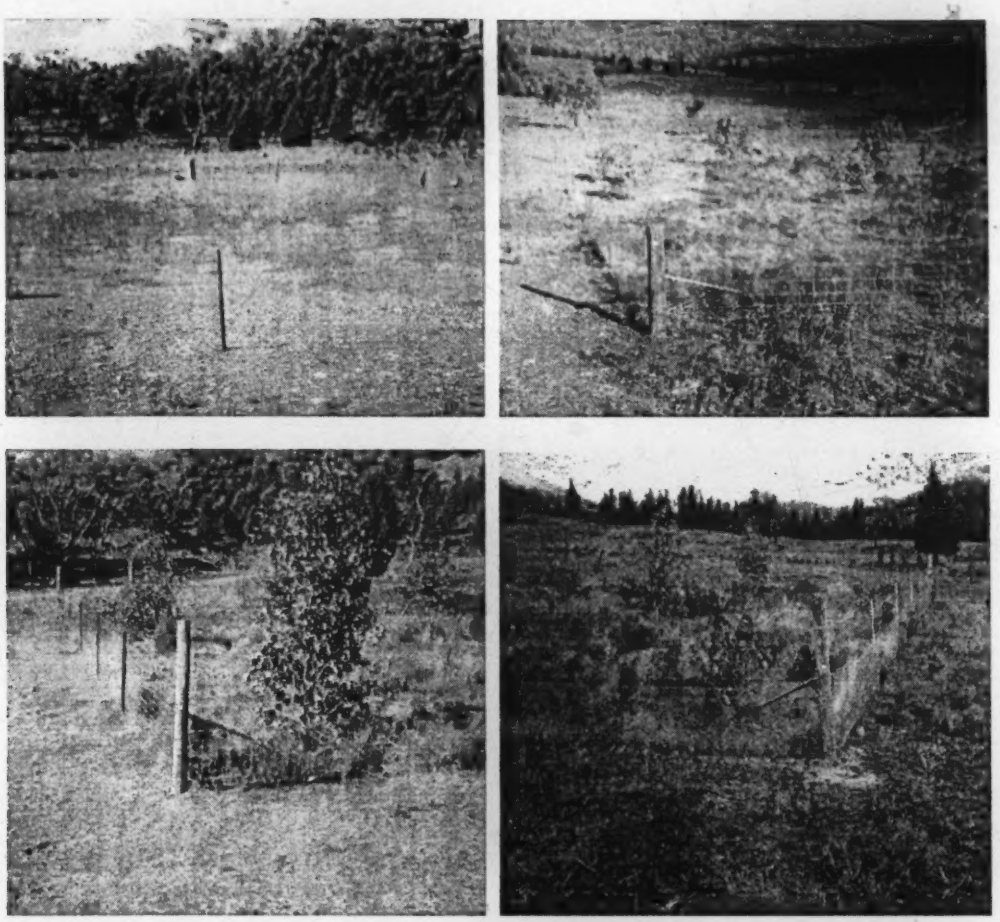

Figure 1.7: Four fencing treatments established at Burrendong Dam NSW. Top left, unfenced control; top right, plain wire stock fence; bottom left, welded wire kangaroo fence; bottom right, welded wire/rabbit wire complete exclosure. Photos courtesy of S. Henry (CSIRO Sustainable Ecosystems).

Chapter 2

Survival, growth and strategies for escape from herbivory of three native Australian woodland plants[1]

Introduction

Vertebrate herbivores have substantial impacts on many plant communities and populations (Crawley 1983, Huntly 1991). Direct mortality is most likely at the seedling stage, but sub-lethal effects of herbivory also influence recruitment and subsequent reproduction of individuals in the population (Crawley 1983). Mortality is not necessary for herbivores to have a dramatic impact on plant populations if herbivory prevents individuals from reaching maturity (e.g. Zamora *et al.* 2001). Plants may "escape" herbivory by growing vertically until their apical meristems are out of reach of herbivores. Once this height threshold is reached, herbivore damage is often minimal, survival is greatly improved, and reproduction becomes more likely (e.g. Sharrow and Fletcher 1994, Zamora *et al.* 2001, Bartolome *et al.* 2002). We refer to this as "escape height".

Different guilds of herbivores, particularly ones that are very different in size or which exhibit differences in behavior or preferences, may have widely varied effects on vegetation (Crawley 1983, Bowers 1993, Ritchie and Olff 1999). Seedlings exposed to different herbivores may show different rates and/or proportions of individuals escaping. The effects of herbivory on a plant's ability to reach escape height are expected to vary

[1] Manuscript currently being formatted for submission to *Oecologia*

among habitats because of differences in growth rates, competitors, and herbivore behavior (Hulme 1996, Zamora *et al.* 2001, Puettmann and Saunders 2001).

In Australian temperate woodlands, including the white box (*Eucalyptus albens* Benth.) woodlands of New South Wales and Victoria, grazing by a variety of herbivores is a major threat to native plant communities (Prober and Thiele 1995, Sivertsen and Clarke 2000). White box woodlands once formed a continuous band along the western side of the Great Dividing Range, but now comprise less than 0.01% of their original extent and have been reduced to small remnants in an agricultural or pastoral matrix (Prober and Thiele 1993). Existing large remnants are often grazed by sheep and cattle, and may be partially cleared. In addition, feral rabbits (*Oryctolagus cuniculus*) and native macropods, particularly eastern grey kangaroos (*Macropus giganteus*) and euros or wallaroos (*M. robustus)* are common. Proposed management of remnants often involves grazing reduction, which usually consists of removal of domestic stock, and sometimes control of feral animals (Hobbs and Yates 2000). Although there is substantial evidence that macropods, sheep, and rabbits differ in forage preferences, feeding modes, and intake requirements (Short 1985, Leigh *et al.* 1989, Freudenberger 1995), the relative effects of these different herbivores on vegetation is poorly understood.

Exclosure studies have proven useful in determining the relative effects of different suites of herbivores on individual plant species (e.g. Hulme 1996, Cid *et al.* 1991, Hester *et al.* 2000) and in assessing the implications of herbivory for the conservation of plant species in systems where herbivores can be managed. We used an array of exclusion fences in remnant white box woodland to assess the effects of habitat and herbivores (sheep and cattle, kangaroos, and rabbits) on the survival and growth of three common

native species (two trees and one grass). Fences and unfenced controls were placed in moderately degraded woodland remnants or grassland (cleared woodland) habitats, and seedlings were planted within each exclosure and control plot in April 1998. Survival and growth of seedlings were monitored from April 1998 to April 2001. These data were subsequently used to model the expected rates of escape from herbivory for seedlings of tree species under different grazing regimes within the two habitat types. Specifically, we addressed three questions:

1. How do survival and growth of native woodland seedlings differ in the presence of different herbivores and in woodland and grassland habitats?
2. Do the effects of herbivory and habitat on survival and growth alter the proportion of tree seedlings able to reach escape height?
3. Is the caespitose perennial grass, *Themeda australis*, able to escape herbivory through increased growth, and what is the relationship between herbivory and persistence for this species?

Methods

Burrendong Dam study area

The experiment was conducted in the Central West Slopes region of New South Wales, Australia, in an area dominated by white box woodlands. Historically, these woodlands consisted of widely spaced mature trees over an understory of caespetose perennial grasses such as *Themeda australis* (R. Br.) Staph. and *Poa sieberiana* Staph., and a variety of annual and perennial herbs growing between grass tussocks. However, very little woodland remains undisturbed (Prober and Thiele 1993, Thiele and Prober

2000). Most wooded areas have been cleared or thinned to create cropland or improved pasture, and grazing by sheep and cattle is currently a primary land use in larger tracts of both cleared grasslands and intact remnant woodlands (Thiele and Prober 2000).

Our study site was located on the eastern foreshores of Burrendong Dam, at the confluence of the Cudgegong and Macquarie Rivers (32° 40' S, 149° 6' E). The site is part of a large catchment administered by the Department of Land and Water Conservation of New South Wales. The climate is temperate with warm summers (mean maximum temperature 29° to 33°C) and cool winters (mean minimum temperature 2° to 3° C), and median annual rainfall of approximately 666 mm (Bureau of Meteorology, 1998). Grassy white box woodlands once dominated the lower slopes, but large areas were cleared in the 1800s to promote pasture growth and the area is now a mosaic of grassland and remnant woodland. In grassland areas the vegetation is usually dominated by native perennial grasses, in particular *Bothriochloa macra, Austrodanthonia spp.* and *Austrostipa scabra*. In spring, many areas are dominated by *Echium plantagineum, Vulpia spp, Bromus spp.* and other annual exotic species; cover of these species can exceed 75%. Vegetation cover is generally 50%-75%, but can be under 10% in heavily grazed areas, or 100% in spring when exotic annual species are abundant. In woodland areas the understory is primarily composed of *Bothriochloa macra, Austrostipa scabra,* and *Austrodanthonia spp.* along with common forbs such as *Dichondra repens*. In spring exotic annual species, in particular *Stellaria media, Lolium rigidum, Vulpia spp., Echium plantagineum,* and *Hypochaeris glabra* can be very abundant, with 50%-100% cover. In summer, total vegetation cover in wooded areas is less than 10% under tree canopy and approximately up to 60% in gaps (K. Allcock, unpublished data).

Sheep and cattle are grazed under license, and eastern gray kangaroos are common. Euros or wallaroos and swamp wallabies (*Wallabia bicolor*) are also present. Prior to July 1996, European rabbits were extremely abundant. Rabbit hemorrhagic disease (RHD) arrived at Burrendong Dam in 1996 and reduced the rabbit population by approximately 90% (Saunders *et al.* 1998). However, rabbits remained relatively common during the period of our experiments (five sightings per spotlight kilometer: A. Newsome and D. Hik, unpublished data).

Experimental design

In February 1997, we constructed a series of 25m by 25m exclosure fences to investigate the impact of grazing on vegetation. The fences were built in two habitats: grassland, which was once white box woodland but in which trees were cleared in the late 1800's to improve pasture production; and woodland, where the *Eucalyptus albens* canopy was intact. We used four grazing treatments. The control plots were unfenced and all vertebrate herbivores could enter them (designated +r +k +s, where r indicates rabbits, k, kangaroos, and s, stock). The stock exclusion plots were fenced with 1.5m tall plain wire stock fences to exclude sheep and cattle (+r +k -s). The kangaroo exclusion plots were fenced with 2m tall welded wire mesh, and excluded sheep, cattle and kangaroos (+r -k -s). The complete exclosure plots were fenced with 2m tall welded wire mesh with a skirt of rabbit wire around the lower portion of the fence that projected outward and was buried to a depth of 20 cm, thereby excluding sheep, cattle, kangaroos, and rabbits (-r -k -s). These treatments are illustrated in Chapter 1, Figure 1.7.

In total, we had four treatments (including unfenced controls), replicated in four blocks each including two habitat types, with blocks distributed over an area of approximately 40 km^2, for a total of 32 experimental plots. The distance between blocks was at least 1 km. Within each block woodland and grassland plots were usually separated by 0.5-1 km, and within each habitat the distance between the four grazing treatments usually ranged from 50 m to 200 m.

Focal species

We selected *Eucalyptus albens, Callitris glaucophylla* J. Thompson and L. A. S. Jonson, and *Themeda australis* as focal species in this experiment in order to allow us to examine different strategies of responding to herbivory. *Eucalyptus albens* (white box) is the dominant canopy tree, but appears to have moderate to poor regeneration at Burrendong. *Callitris glaucophylla* (cypress pine) is a canopy or sub-canopy species that is sometimes considered a woody weed. At Burrendong it successfully regenerated over large areas in the 1960's (following de-stocking and rabbit control). *Themeda australis* (kangaroo grass) is a tall, warm season, caespitose grass that was once the dominant understory species in white box woodland, but has been nearly extirpated from the Burrendong site because of heavy grazing.

We planted seedlings each species rather than relying on natural regeneration in order to follow a known-age cohort through the course of the experiment. Tree seedlings of local stock were purchased from the New South Wales Forestry Nursery in Dubbo NSW, and were between 15 and 30 cm tall at the time of planting. Plugs of *T. australis* (approximately 1 to 2 cm basal diameter and 10 to 15 cm tall) were purchased from A-

Bulk Pty. Ltd., Sydney. Twenty seedlings of each species were planted approximately 3m apart in a regular grid in each experimental plot. In order to minimize disturbance of soil and neighboring vegetation when planting tree seedlings, we used a soil auger to create holes approximately 10 cm in diameter and 20 cm deep. For grass plugs we created small holes (three cm diameter) using a steel fence post. To minimize disturbance while performing subsequent measurements, plants were accessed from paths approximately 1m from the seedlings. We used plastic shields to protect seedlings from herbivory for four days after planting, and then removed the shields to begin the experiment. *Themeda australis* seedlings were planted in April 1998, and *E. albens* and *C. glaucophylla* seedlings were planted in May 1998.

Monitoring

For the first month of the experiment, seedlings were checked every two to three days, and thereafter every one to two months until April 1999. We recorded survival, signs of herbivory, species of herbivore responsible if it could be determined, cause of death for plants not surviving, and plant height. Bite marks were distinctive for each herbivore species. Rabbits clipped stems cleanly at a 45° angle and often scratched or dug at the base of the plant, kangaroos stripped leaves and branches from seedlings and left tall stems (10-15 cm tall) with ragged or broken tops, sheep browsed or grazed to a short height (<5 cm) and left ragged tops on broken stems, and cattle broke stems raggedly and often uprooted or trampled plants. If there was any ambiguity in the interpretation of bite marks, herbivory was attributed to an unknown herbivore. Seedlings were checked and measured for a final sample in April 2001, three years after planting.

Standing biomass of vegetation in each plot was measured in spring and autumn each year. Standing vegetation was clipped at ground level in 12 randomly located circular plots 7 cm in diameter. Samples were pooled for each exclosure, dried for 48 hours at 80° C, and weighed. Biomass estimates from spring of 1998 were included as a predictor variable in statistical analyses of transplant survival because target seedlings were still small enough at this time to experience severe competition for light and space with rapidly growing herbaceous plants.

Animal activity in the experimental plots was monitored in March and April 1998 using faecal pellet counts in ten permanent $1m^2$ quadrats. The quadrats were cleared of all pellets one month prior to initial sampling (i.e. in February 1998), and pellets falling within quadrats at the time of sampling were counted and removed. Pellets were sampled monthly until vegetation became too dense for accurate counts (last sampling April 1998). Within the entire study area, spotlight counts of herbivores in the study area were conducted approximately each month throughout the course of the experiment (A. Newsome and D. Hik, unpublished data). While both pellet and spotlight counts were used to assess the effectiveness of the treatments, they were inadequate to reflect the variation in herbivore activity at the scale of individual plots. Therefore, we determined the cumulative number of plants browsed that could be attributed to each species of herbivore over the course of the experiment to provide a quantitative measure of the effectiveness of the exclosures, as well as an index of the activity of each species in the experimental treatments.

Data Analysis

Survival - Logistic generalized linear models (S-Plus 2000, Mathsoft Inc. 1999) were used to analyze the proportions of seedlings surviving through April 2001. Treatment, habitat, block, and standing biomass in October 1998 (spring of the first year after planting) were used as predictor variables. It was not possible to test all interactions because of limited degrees of freedom, but the treatment by habitat interaction and all two-way interactions involving block were included. In all cases, block was added to the model first to account for block-related variance, thereby ensuring that estimates of the effects of other variables were conservative (S-Plus 2000 Online Documentation, Mathsoft Inc. 1999). Data for each species were analyzed separately.

Assessment of mortality focused on the general patterns of survival in the different treatments, rather than detailed causes of mortality for each species in each treatment. While specific causes of mortality were helpful in determining the effectiveness of the treatments for the purposes of the current analyses (see above), this detail was less relevant for interpreting the overall effects of herbivory on survival, growth, and escape.

Final height - The height of each surviving plant was measured in April 2001. A two-way nested ANOVA for each species with habitat and treatment as main factors was used to address variation in plant height. For *Themeda*, separate one-way analyses were performed for woodland and grassland plots because some grassland treatments had no surviving individuals. For all analyses, height was log-transformed to ensure homogeneity of variance.

Escape threshold - To predict the influence of habitat and grazing treatment on the potential for tree seedlings to reach escape height, we used the results of our transplant

experiment to construct a series of stage (size-class) based matrix models with a stochastic component (Caswell 2001). The number of individuals entering a given size class for time (t+1) was determined by sampling from a random distribution with mean P (probability of moving to a given size class based on our empirical data) to obtain a value for p (probability of "success" in a binomial distribution), and then sampling from a binomial distribution with parameter p to determine the number of trees moving to a new size class in time (t+1) given the number from original size class at time (t).

We defined five height classes: <25 cm, 25-49 cm, 50-74 cm, 75-100 cm, and >100 cm (escape threshold). Although this height was within the reach of browsing cattle, no tree seedlings over one metre tall showed evidence of herbivore damage. In addition, any plants reaching one metre in height grew very rapidly to two or more metres within one growing season. We constructed models for *C. glaucophylla* and *E. albens* seedlings in each habitat and treatment combination, for a total of 8 models per species.

The matrix models for *E. albens* and *C. glaucophylla* consisted of two components. Matrix One (M1) described the probability of seedlings in size class two (25-29 cm, equivalent to our tubestock transplants) moving into any of the other size classes in the first year of growth. All transition probabilities were calculated from growth and survival data from year one of our field experiment. Matrix Two (M2) included all possible transitions between stages, as illustrated in Fig. 2.1, and used a two-year time step in which transition probabilities were based on observed survival and growth of transplants in years two and three of our experiment.

The models were run with an initial cohort of 1000 individuals in size class two (to represent an attempt to establish trees by planting tubestock). Multiplication by M1

predicted the size class distribution after the first year of growth, and then M2 predicted the size class distribution and the number of individuals reaching escape height over the next 14 years. Each model was run 20 times, and the mean outcomes are presented (Figure 2.5).

For cells in M2 where no transitions were observed in the field, probabilities were determined in one of two ways. If the transition was deemed unlikely (for example, reversion from "escape" to any of the other size classes, or transition from class one to class five in one time step) we used a value of 0.001 as the transition probability. However, if the transition was likely or possible, but was not observed because of the time scale of the experiment (for example, transition from class 4 to class 5) we assumed approximately constant transition rates to adjacent stages for all size classes. Specifically, we extrapolated the diagonals of the matrix to estimate probabilities, and adjusted these upward by a value of 0.05 for larger size classes to allow for higher survival of larger individuals.

Results

Herbivore activity in experimental treatments

Overall, we are confident that our experimental fences were effective. Faecal pellet counts conducted in March and April 1998 indicated little difference in animal activity across similar grazing treatments, and fences were effective in excluding the species they were intended to exclude (Table 2.1). Animal activity was generally greater in grasslands, however the dung counts did not provide a good estimate of stock activity.

Nevertheless, stock were regularly observed in the vicinity of unfenced plots during monthly spotlight surveys.

Table 2.2 shows the proportions of individual plants in each treatment and habitat that experienced herbivory by each species of herbivore over the course of the experiment. These herbivory events do not necessarily translate to mortality, and some individuals were browsed more than once, resulting in some proportions over 100%. In general, herbivory by stock was greater in grassland, while rabbit and kangaroo herbivory were more frequent in woodlands. For *T. australis,* rabbit and kangaroo herbivory were similar in both habitats. There is some indication that kangaroos were less active in stock fences than in controls, with more herbivory events attributed to kangaroos in controls than in stock fences and more dung pellets counted in unfenced plots (Tables 2.1 and 2.2). Rabbits consumed a larger proportion of seedlings in plots with other herbivores excluded, but overall herbivory was reduced with increasing level of exclusion.

Differences in above-ground biomass

Two-hway ANOVA on log-transformed biomass measurements showed that above-ground biomass in April 1998 differed significantly between habitats ($F=17.8$, $p<0.001$) and between treatments ($F=5.03$, $p<0.001$) with no interaction ($F=0.28$, $p=0.84$). Biomass was higher in treatments to which fewer herbivore species had access (the rank order was +r+k+s < +r+k-s < +r-k-s < -r-k-s), and Tukey multiple comparisons showed that unfenced (+r+k+s) plots had significantly lower biomass than either kangaroo-stock exclosures (+r-k-s) or complete exclosures (-r-k-s). Average above-ground biomass was 84.4 g/m^2 (±18.4 S.E.) in woodlands and ranged from 38.4±16.3 g/m^2 in unfenced plots

to 140±57.2 g/m^2 in complete exclosures. Average above-ground biomass in grasslands was 342.6 g/m^2 (± 84.0 S.E.) and ranged from 81.9±20.6 g/m^2 in unfenced plots to 510.9±190 g/m^2 in complete exclosures.

Survival of transplanted seedlings

The effect of excluding different suites of herbivores on patterns of survival differed among habitats and plant species (Fig. 2.2). Generally, survival was greatest in plots with no grazing, but differences between habitats and species were apparent. Survival was greater in woodlands than in grassland sites, with the exception of tree seedlings in unfenced woodland plots. For *C. glaucophylla*, plants in unfenced plots had the lowest survival (approximately 20%), a trend that was more obvious in woodland plots. For *E. albens*, plants in unfenced plots had lower survival in both habitats than did plants in any fence treatment (40-50% in controls compared to 70-90% in fences). For *T. australis* survival in grasslands was very low (less than 30%) in all treatments except the complete exclosure (approximately 60%), while in woodlands, plants in both complete exclosures and kangaroo-stock exclosures had higher survival (60-70%) than plants in stock fences or unfenced plots (10-30%).

An analysis of survival for each species, using generalized linear models, is presented in Table 2.3. For *E. albens*, fence type was the most significant predictor of survival, explaining almost half of the variance, followed by habitat. Simultaneous 95% CIs for fence type (Sidak Method, S Plus 2000, MathSoft Inc. 1999) showed that survival of *E. albens* in unfenced plots was significantly lower than survival in any of the other treatments. Density of the herbivores, and consequently mortality due to herbivory,

differed somewhat across the study area resulting in a significant block by treatment interaction. However, the pattern of survival among the four treatments was consistent across all blocks despite higher overall mortality in some blocks, providing some confidence in our interpretation of the confidence intervals.

For *T. australis,* block, fence type, habitat, and log (biomass) all contributed significantly to the survival model, with no significant interactions (Table 2.3). Fence type explained the most variance in survival (46%), followed by biomass (30%), block (9%), and habitat (2%). Simultaneous 95% CIs for fence type showed that plants in controls and stock fences had significantly lower survival than in kangaroo and complete fences. Survival was greater in woodland plots than in grassland plots, and there was a negative relationship between survival and log (biomass).

For *C. glaucophylla*, block, fence type, and log (biomass) were all significant predictors, but there was also a significant block by treatment interaction (Table 2.3). Survival did not differ significantly between habitats. Fence type explained the most variance (29%) followed by the block by type interaction (17%), block (7%), and log (biomass) (10%). Simultaneous confidence intervals for fence type showed significantly lower survival in unfenced plots than in complete exclosures. As with *E. albens*, the pattern of survival among treatments was similar across blocks, though overall mortality was not.

Final height of surviving transplants

Figure 2.3 shows the height of surviving transplants (averaged across blocks, weighted by number of surviving individuals in each experimental plot) in each habitat-

treatment combination over the course of the experiment. In all cases, plants in fenced treatments were taller than in controls, heights were generally greater with increasing levels of protection, and differences between treatments were greater in grassland than in woodland. Differences in height between treatments were small after the first year of growth, but increased towards the end of the experiment. For *E. albens,* both stock and kangaroos had an effect on height, particularly in grassland plots, while rabbits appeared to have little influence. In grasslands, *E. albens* plants in controls and stock fences were 30% and 50% as tall respectively as *E. albens* in kangaroo/stock exclosures or complete exclosures. For *C. glaucophylla,* stock had the greatest impact, especially in grasslands. Plants in control plots were 50% as tall as plants in complete exclosures. For *T. australis*, exclusion of stock and kangaroos resulted in increased height, with heights two or three times as high as heights in the controls, respectively. Excluding rabbits had little effect on the height of *T. australis.* Seedling heights at the end of the experiment are summarized in Figure 2.4.

Analyses of variance on height showed strong effects for both habitat and grazing treatment. For *E. albens*, both fence type and habitat were highly significant (Table 2.4), and there was no interaction. Plants were taller in grassland plots, and *a-posteriori* analyses (simultaneous confidence intervals, Tukey method) showed significant differences in plant height between all treatments except stock/kangaroo fences (+r -k -s) and complete exclosures (-r -k -s). For *C. glaucophylla*, both treatment and habitat were highly significant. However, there was a significant treatment by habitat interaction, so two one-way ANOVAs were subsequently performed (Table 2.4). Trees in grassland plots were taller than those in woodlands. Multiple comparisons showed that in

grasslands trees from unfenced plots were significantly shorter than trees from any fenced plot. In woodlands, trees in control plots were significantly shorter than any other treatment, trees in stock fences and stock/kangaroo fences were not significantly different in height, and trees in complete exclosures were significantly larger than those in any other treatment.

For *T. australis,* size was significantly affected by treatment within woodland plots, but not in grassland plots (Table 2.4). However, there were no individuals surviving in either controls or stock fences in the grassland, and there were only two kangaroo fences and three complete exclosures with surviving individuals of *T. australis.* Multiple comparisons of heights in woodland plots showed that individuals in unfenced plots were significantly smaller than individuals in any other treatment, and plants in stock fences were smaller than those in stock/kangaroo fences or complete exclosures.

Modeling escape height of trees

Removal of some or all of the herbivores greatly increased the predicted proportion of *C. glaucophylla* and *E. albens* seedlings reaching escape height (>100cm) over a 15-year run of the matrix models for each habitat and grazing treatment (Fig. 2.5). The rate of escape was generally greater in grassland habitats (with the exception of *C. glaucophylla* in woodland complete exclosures). These individuals also reached escape height 3-5 years earlier. In woodlands, less than 0.5% of individuals escaped without exclusion of at least some herbivores.

Differences in escape between fencing treatments and in different habitats were also evident. For *C. glaucophylla* in grassland, exclusion of stock and exclusion of all

herbivores resulted in increased escape (approximately a 20% increase and a 100% increase over unfenced plots, respectively), but exclusion of kangaroos without excluding rabbits had little effect. In woodlands, the reduction in escape rate induced by grazing animals was much more pronounced than in grassland, and excluding rabbits had the largest influence (approximately a 100% increase over the kangaroo/stock exclusion treatment). For *E. albens* in grasslands, excluding stock allowed a large increase in escapes, while there was little additional response to excluding kangaroos, and no response to rabbit exclusion. In woodlands, excluding stock increased escape from almost zero to approximately 30%, and the effect of excluding kangaroos was much more dramatic than in grasslands (a 100% increase in survival over stock exclusion in woodlands, versus less than 10% in grasslands). Again, excluding rabbits had little effect on the rate of escape for *E. albens*.

Size and reproduction in T. australis

We did not construct models for *T. australis,* because as a caespitose grass its meristems are always within the reach of herbivores, and escape height is less meaningful. However, greater leaf height and greater tussock diameter may convey some degree of protection to the meristems, and larger, taller plants were more likely to reproduce. To investigate these patterns, we examined the relationship between height, basal diameter, and flowering for *Themeda* individuals surviving until April 2001.

There was a strong positive relationship between leaf height and basal diameter for *T. australis* plants surviving until April 2001 (Fig. 2.6). Pearson's correlation coefficients were 0.78 for untransformed data and 0.88 when basal diameter was log-transfomed.

Larger plants were more likely to produce flowers, and only individuals that showed little or no sign of herbivore damage flowered during the course of the experiment. We conducted a logistic regression to determine the relationship between probability of flowering and plant height. There was a highly significant positive relationship between height and probability of flowering ($p<0.0001$ for 147 df). Height explained 48% of variation in flowering. Based on the parameter estimates (intercept = -4.1±0.8 SE; height= 0.14±0.02 SE), the model predicted that plants under 30 cm in height had less than a 50% probability of flowering. Plants were larger in grassland plots and in plots with at least some protection from herbivory. No plants in unfenced plots flowered and only one individual flowered in the treatment where only stock were excluded.

Discussion

Survival

This experiment demonstrated pronounced differences in survival rates between seedlings of the same species grown in different habitats or accessible to different grazing animals. In all cases, exclusion of successively smaller herbivores resulted in an increase in overall survival. Survival in woodlands was greater in almost all treatments compared to corresponding survival in grasslands. Death of seedlings of all species in grasslands was often due to overgrowth by surrounding herbaceous vegetation, primarily introduced annuals, particularly during the first three months following transplantation (Table 2.2). In plots with herbivores excluded, overgrowth was the most common cause of mortality, while in grazed plots overgrowth was unlikely. Increasing survival with increasing exclosure suggests an additive effect of the different herbivore types on survival of the

species tested (Ritchie and Olff 1999). However, herbivores consumed not only the target seedlings but also surrounding herbaceous vegetation, apparently reducing competition for the target species and producing some degree of compensation, although this compensation did not overcome the generally negative effect of herbivory.

The degree to which exclusion of each herbivore increased survival differed between plant species and habitats, indicating differences in the susceptibility of the plant species and preferences of the herbivores. The individual effects of each herbivore species in this study cannot be strictly determined because the design used did not allow grazing by each herbivore in isolation. However, by comparing the survival of seedlings in treatments with and without particular herbivores, it is possible to observe their relative effects. For *E. albens*, exclusion of stock increased survival substantially while each additional level of exclosure had a negligible impact, and this pattern held in both woodland and grassland. For *C. glaucophylla* each level of exclusion increased survival slightly, and the effects of stock were more pronounced in the woodland habitat. For *T. australis*, herbivory and habitat both had a major impact on survival. In grasslands, only exclusion of all herbivores allowed an increase in survival, indicating that all herbivores had a strong negative impact on *T. australis*. In woodlands, excluding stock increased T. australis survival slightly, excluding kangaroos allowed a large increase in survival, and excluding rabbits did not affect survival, indicating that kangaroos were the most important herbivores of *T. australis* seedlings in woodlands.

There were also fundamental differences in survival between the different plant species. *E. albens* had high survival overall, perhaps because of its ability to re-sprout. *C. glaucophylla* showed moderately high survival, but survival was negatively affected

by all grazing species. *T. australis* had low survival especially in the presence of herbivores, and was also susceptible to overgrowth. Because of the short life span of *T. australis* (about five years before it must reproduce by seed: Belsky 1986) and the level of mortality observed in the presence of all vertebrate herbivores in this experiment, mortality of seedlings is likely a very important mechanism behind the decline of this species under sustained grazing.

Growth

Seedling height was also influenced by both herbivory and habitat, but did not always reflect the same patterns as survival. Differences in shoot growth were not obvious at the end of the first year (when differences in survival were already observed), but were substantial by the end of year three. It is possible that in the first year of growth seedlings allocated more resources to establishing root systems, and then in subsequent years were able to devote more resources to shoot production.

Seedlings of all species were considerably larger in grasslands than in woodlands by the end of the experiment. In fact, for *E. albens* and *C. glaucophylla*, the benefit of being in the grassland habitat seemed to compensate for the negative effects of herbivory: in both cases, grassland seedlings in the unfenced plots were nearly identical in size to woodland seedlings in complete exclosures. Grasslands have more available light and competition for water might be lower (e.g. Yates *et al.* 2000) than in woodlands. The ability of plants to recover more quickly from herbivory in high resource environments has been noted previously (e.g. Tilman 1988, Jefferies *et al.* 1994, Ritchie and Wolfe 1994, Hulme 1996).

There were differences among the three plant species tested in their growth responses to the herbivory treatments, and the patterns of final height were not the same as the patterns of final survival. For *E. albens*, excluding stock allowed a substantial height gain, as did excluding kangaroos, while excluding rabbits had little effect. This result contrasts with the pattern of survival, where only exclusion of stock had an impact. For *C. glaucophylla*, exclusion of stock resulted in taller trees, while exclusion of kangaroos had little effect, and exclusion of rabbits resulted in another increase in final height in woodlands. For *T. australis*, height of surviving individuals in grasslands was not affected by the presence of rabbits, although rabbits reduced survival. The effects of stock and kangaroos on growth in grasslands could not be assessed, and indeed may be inconsequential, because of their very strong effect on survival. In woodlands, the pattern of *T. australis* heights was similar to the pattern of survival, with both stock and kangaroos (especially kangaroos) having a negative impact, and little effect of rabbits.

Escape

Because herbivores and habitat influenced patterns of growth and patterns of survival differently, both growth and survival must be included when assessing the effects of multiple herbivore species on plant regeneration. The models we used to predict the proportion of escapes incorporate the growth and survival responses we observed. The results must be interpreted carefully since transition rates between size classes were assumed to be constant from years 2-15; however, the models permit some specific predictions concerning herbivore management that were not obvious by examining survival or growth alone.

Seedlings reached escape height much more rapidly in grasslands (three to five years) than in woodlands (seven to ten years). The final proportions escaping were almost always lower in woodlands than in grasslands, although woodland survival rates were higher overall. The slower growth rates in woodland habitats meant that seedlings stayed in susceptible size classes longer, with higher risk of death or retrogression to a smaller size class. The rapid growth rate in grasslands ameliorated some of the negative effects of herbivory, and the predicted effects of the herbivore treatments were much more pronounced in woodlands than in grasslands. In a habitat where growth is rapid and/or productivity is high, herbivory may have a minimal impact on recruitment because individuals can rapidly reach a size at which herbivory becomes less harmful. In contrast, the models predicted no escape of either *E. albens* or *C. glaucophylla* in woodlands grazed by all herbivore types; even with partial herbivore control, escape was low.

Other researchers have noted that even intense herbivory does not always affect regeneration or population size (Foran 1986, Tiver and Andrew 1997). However, both lethal and sublethal effects of herbivory would be most likely to affect regeneration in areas of low productivity and/or slow growth where individuals remain susceptible to herbivory for an extended period (e.g. Zamora *et al.* 2001). Productivity gradients are important to consider in management of remnant eucalypt woodlands. *Eucalyptus albens* seeds do not tend to disperse long distances (Clatyon-Greene and Ashton 1990) and thus most natural regeneration would occur in patches near healthy adult trees. Seedlings in these stands would have slower growth rates than in open areas, implying that herbivore management would be essential for successful recruitment.

The models also indicated that controlling different species of herbivores could affect escape differently, and that *E. albens* and *C. glaucophylla* may not respond in the same way to herbivore control. Escape of *Eucalyptus* was most strongly affected by removal of stock and kangaroos; subsequent removal of rabbits had no effect. While this result does not mean that rabbit control in the presence of sheep and/or kangaroos would be completely ineffectual, it does suggest that removal of stock or kangaroo control might result in a larger increase in *E. albens* escape, whereas rabbit control might favor encroachment of *C. glaucophylla* in remnant white box woodlands.

While growth rate was a driving factor in potential escape and population maintenance of long-lived *E. albens* and *C. glaucophylla*, survival was much more important for the shorter-lived grass, *T. australis*. The concept of "escape height" makes little sense for a species with meristems at ground level and foliar heights of less than one meter. However, size is related to reproduction and survival. In this experiment, larger plants were more likely to produce flowers within three years, and only individuals that had never been visibly grazed produced flowers. In addition, a larger tussock, taller leaves, and/or more tillers would afford some protection to the meristems.

Given that *T. australis* has meristems at ground level, it may have a reduced capacity to produce seed when grazed, and in fact the seed bank of *Themeda* in Africa is easily eliminated by sustained grazing (O'Connor and Pickett 1992). Because of its short (<10 year) life span, caespetose life form, susceptibility to grazing, and reliance on seed for population maintenance *Themeda* has been considered an extinction prone grass under sustained grazing (O'Connor 1991) and *T. australis* is known to disappear under sustained grazing (e.g. Moore 1970). In our study, grazed plants tended to be smaller and

potentially more susceptible to further damage by grazing, seedling mortality was higher, and probability of flowering was lower for grazed and/or small plants. However, our study found that *T. australis* seedlings were susceptible to overgrowth (primarily by exotic annual weeds) in the absence of herbivory, and there was a negative relationship between survival and standing biomass of surrounding vegetation. Regeneration of *T. australis* and native caespetose grasses with similar life history characteristics cannot be managed solely by reducing grazing pressure, especially if only some herbivore species are controlled; management of fast-growing exotic species will also be necessary.

Differential Effects of Herbivores

This experiment illustrates the complexity of multi-species plant-herbivore interactions. Differences in both herbivore behavior and susceptibility of plant species were apparent. For example, stock showed a preference for *E. albens* seedlings and were very active in grassland plots. Rabbits and kangaroos were more active in woodlands, and rabbits preferred *C. glaucophylla*, while kangaroos damaged primarily *E. albens* and *T. australis*. These differences have the potential to affect plant composition at the community level, particularly if partial herbivore control is implemented.

Many studies of herbivory have found or predicted similarly complex results. Ritchie and Wolfe's (1994) simulation model of herbivory by deer, elk, and cattle predicted different plant community composition under different management schemes, and illustrated the importance of indirect effects on community level results of herbivory. Differences in the effects of herbivory on survival, growth, recruitment, and/or

regeneration of different plant species have frequently been presented (Hodgekinson *et al* 1989, De Steven 1991, Auld 1995, Hulme 1996, Tiver and Andrew 1997).

Some researchers have used exclosure studies similar to the one presented here to determine effects of different herbivores on plant species and community composition (for example, Bowers 1993, Auld 1995, Freudenberger 1995, Hulme 1996). They all found differences, some attributed to herbivore identity (Auld 1995, Hulme 1996) and some merely to differences in grazing intensity (Bowers 1993, Freudenberger 1996). While our study was limited in its ability to tease apart the individual effects of each herbivore species, it provided substantial evidence that both grazing intensity and herbivore identity are important in determining the outcomes of herbivory in multi-species communities. We cannot clearly assess the extent to which the effects of stock, macopods and rabbits are strictly compensatory or additive at Burrendong site, however our approach provides relevant information for grazing management that would maximize the opportunity to re-establish native species.

Conclusions

Survival and growth are both important in determining escape of seedlings, and we found that herbivores affected escape both by reducing survival and by limiting height (growth). The relative importance of reduction in growth versus survival depends on the habitat, the life history of the plant species involved, and the behavior of the herbivores.

Encouragement of *E. albens* regeneration may require removal of stock from wooded remnants for at least five years to allow recruits to reach escape height; in cleared remnants introduction of livestock in combination with shorter-term stock removal

would be appropriate. Encouraging recruitment of *C. glaucophylla* is probably neither necessary nor desired in white box remnants; however any sustained (>5 year) reduction in herbivory, particularly rabbit control, would encourage cypress pine regeneration. *Themeda australis* is susceptible both to herbivory and to overgrowth by surrounding vegetation, and will therefore require careful management. Its short life span, susceptibility to overgrowth, and dependence on regeneration from seed imply that disturbance is necessary to maintain *T. australis* populations; however sustained grazing will cause extinction. Intermittent burning to remove biomass, control of exotic species, re-introduction of *T. australis* plants and a drastic reduction in herbivory may be necessary to re-establish *T. australis*.

While it is possible to make recommendations for each species, developing a management plan for multiple species is more difficult. The effects of herbivory in a system with an array of herbivores are complex and the impacts of different herbivores will differ from plant species to plant species. Effective grazing management in remnant white box woodlands will therefore require careful planning. For example, focusing on stock reduction alone might be adequate to encourage regeneration of *E. albens* especially in open habitats; however, this strategy is unlikely to favor re-establishment of *T. australis* and may not be effective in areas with closed canopy. Similarly, rabbit control alone might favor recruitment of *C. glaucophylla* because stock and kangaroos have a large impact on *E. albens* and *T. australis*, whereas rabbits have the largest effect on *C. glaucophylla*. The choice of management actions will require detailed consideration of the individual taxa and their interactions.

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Table 2.1: Faecal pellets of rabbits, kangaroos, and sheep (per m^2) in March and April 1998. Values are based on pellet counts in 10 permanent quadrats in each experimental plot (mean±SE per $1m^2$ quadrat over two months).

	Grassland			Woodland		
Treatment	Rabbit	Kangaroo	Sheep	Rabbit	Kangaroo	Sheep
+r +k +s	6.10±1.6	9.1±3.2	0	1.75±0.8	2.57±1.1	2.8±2.8
+r +k -s	4.10±1.5	7.4±2.5	0	2.20±1.4	2.14±1.3	0
+r -k -s	7.38±2.5	0	0	2.33±1.5	0	0
-r -k -s	0	0	0	0	0	0

Table 2.2: Percentage of *Callitris glaucophylla, Eucalyptus albens,* and *Themeda australis* seedlings showing signs of herbivory by stock (S), kangaroos (K), rabbits (R), or unidentified herbivores (U) between April 1998 and April 2001. The final two columns present the percentage of seedlings known to have died from overgrowth by surrounding vegetation (OG). Eighty individuals of each plant species were transplanted into each treatment in each habitat. Some individuals were browsed or grazed several times, thus total percentages could exceed 100%.

	Grassland (Gr)					Woodland (Wd)					Overgrown	
Treatment	U	S	K	R	Total	U	S	K	R	Total	Gr	Wd
C. glaucophylla												
+r +k +s	25	33.8	10	27.5	96.3	8.8	5	23.8	62.5	100	0	2.5
+r +k –s	13.8	(1.3)*	5	27.5	47.5	6.3	0	13.8	71.3	91.3	1.3	1.3
+r -k –s	0	0	0	26.3	26.3	0	0	0	82.5	82.5	35	0
-r -k -s	0	0	0	0	0	0	0	0	0	0	43	5
E. albens												
+r +k +s	13.8	55	21.3	13.8	103.8	13.8	16.3	40	27.5	97.5	0	0
+r +k -s	15	(18.8)	18.8	16.3	68.8	21.3	(5)	23.8	26.3	76.3	1.3	1.3
+r -k -s	0	0	0	21.3	21.3	0	0	0	56.3	56.3	12.5	1.3
-r -k -s	0	0	0	0	0	0	0	0	0	0	20	13.8
T. australis												
+r +k +s	43.8	3.8	26.3	23.8	97.5	28.8	7.5	35	15	86.3	8.8	8.8
+r +k -s	23.8	0	32.5	37.5	93.8	16.3	0	32.5	42.5	91.3	23.8	12.5
+r -k -s	0	0	0	62.5	62.5	0	0	0	55	55	53.8	12.5
-r -k -s	0	0	0	0	0	0	0	0	0	0	38.8	11.3

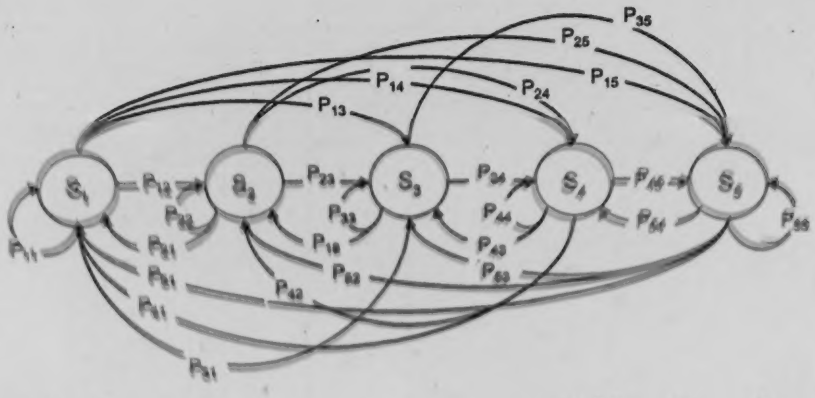
*In June 1998, sheep entered two of the stock fences and damaged some seedlings (indicated by numbers in parentheses). Fences were repaired within one day of the breach and were effective for the remainder of the experiment.

Table 2.3: Generalized linear models of seedling survival after three years for *Callitris glaucophylla*, *Eucalyptus albens*, and *Themeda australis* subjected to four grazing treatments in two habitats.

Species	Variable	DF	Deviance explained (%)	p (Chi)
Callitris glaucophylla	Block	3	7	0.01
	Fence type	3	29	<0.0001
	Log (biomass)	1	10	<0.0001
	Habitat	1	1.6	0.09
	Block x Fence type	9	17	<0.001
Eucalyptus albens	Block	3	1	0.72
	Fence type	3	48	<0.0001
	Log (biomass)	1	<1	0.57
	Habitat	1	8	<0.001
	Block x Fence type	9	24	<0.0001
Themeda australis	Block	3	9.5	<0.0001
	Fence type	3	46	<0.0001
	Habitat	1	2	0.01
	Log (biomass)	1	30	<0.0001

Table 2.4: Analysis of variance of heights (replicate sites and individuals nested within treatments) after three years for *Callitris glaucophylla, Eucalyptus albens,* and *Themeda australis* exposed to four grazing treatments in two habitats. Data have been log-transformed.

Species	Variable	DF	MS	F	P
Callitris glaucophylla Grassland	Fence type	3	2.11	22.46	<0.001
	Nesting	12	0.17	1.85	0.052
	Residual	90	0.09		
Callitris glaucophylla Woodland	Fence type	3	6.44	19.48	<0.001
	Nesting	11	1.1	2.24	<0.001
	Residual	119	0.33		
Eucalyptus albens	Fence type	3	25.74	90.6	<0.0001
	Habitat	1	118.87	418.44	<0.0001
	Fence type x Habitat	3	0.69	2.44	0.064
	Nesting	24	2.79	9.83	<0.0001
	Residuals	24	3.3		
Themeda australis Grassland	Fence type	1	.01	0.62	0.44
	Nesting	3	0.006	0.29	0.83
	Residuals	35	0.02		
Themeda australis Woodland	Fence type	3	6.23	32.3	<0.0001
	Nesting	9	0.9	4.65	<0.001
	Residuals	96	0.19		



Matrix One	S_1	S_2	S_3	S_4	S_5
S_1 [<25 cm]	0	P_{21}	0	0	0
S_2 [25-49 cm]	0	P_{22}	0	0	0
S_3 [50-74 cm]	0	P_{23}	0	0	0
S_4 [75-100 cm]	0	P_{24}	0	0	0
S_5 [>100 cm]	0	P_{25}	0	0	0

Matrix Two	S_1	S_2	S_3	S_4	S_5
S_1 [<25 cm]	P_{11}	P_{21}	P_{31}	P_{41}	P_{51}
S_2 [25-49 cm]	P_{12}	P_{22}	P_{32}	P_{42}	P_{52}
S_3 [50-74 cm]	P_{13}	P_{23}	P_{33}	P_{43}	P_{53}
S_4 [75-100 cm]	P_{14}	P_{24}	P_{34}	P_{44}	P_{54}
S_5 [>100 cm]	P_{15}	P_{25}	P_{35}	P_{45}	P_{55}

Figure 2.1: Stages and transitions for stage-classified matrix models for *Callitris and Eucalyptus*. In the first iteration (one year time step), only transitions involving S_2 were included (Matrix One). In all subsequent iterations (two year time step), all possible transitions were included (Matrix Two).

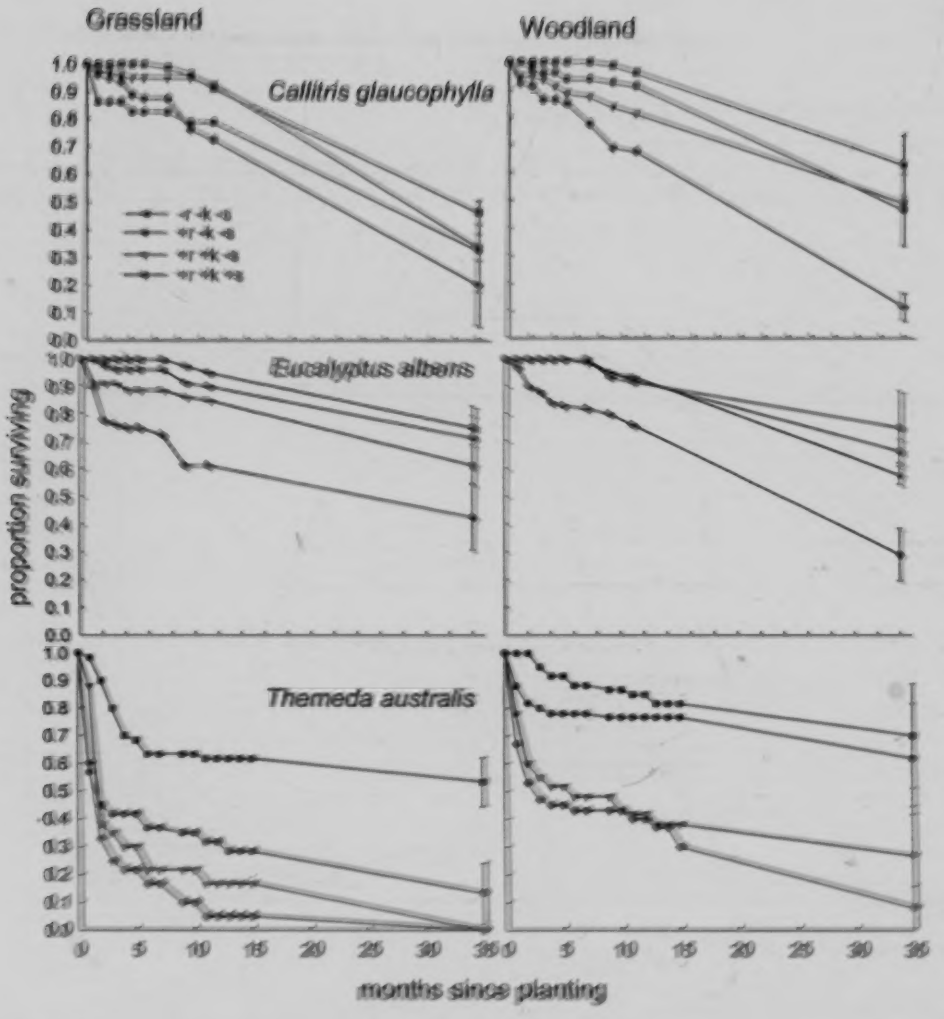


Figure 2.2: Average monthly survivorship of *Callitris glaucophylla*, *Eucalyptus albens*, and *Themeda australis* seedlings in grassland and woodland, under four grazing treatments: all herbivores present (+r +k +s), stock excluded (+r +k -s), stock and kangaroos excluded (+r -k -s), and all herbivores excluded (-r -k -s). Error bars are one standard error, and have been omitted from all but the final survivorship for clarity.

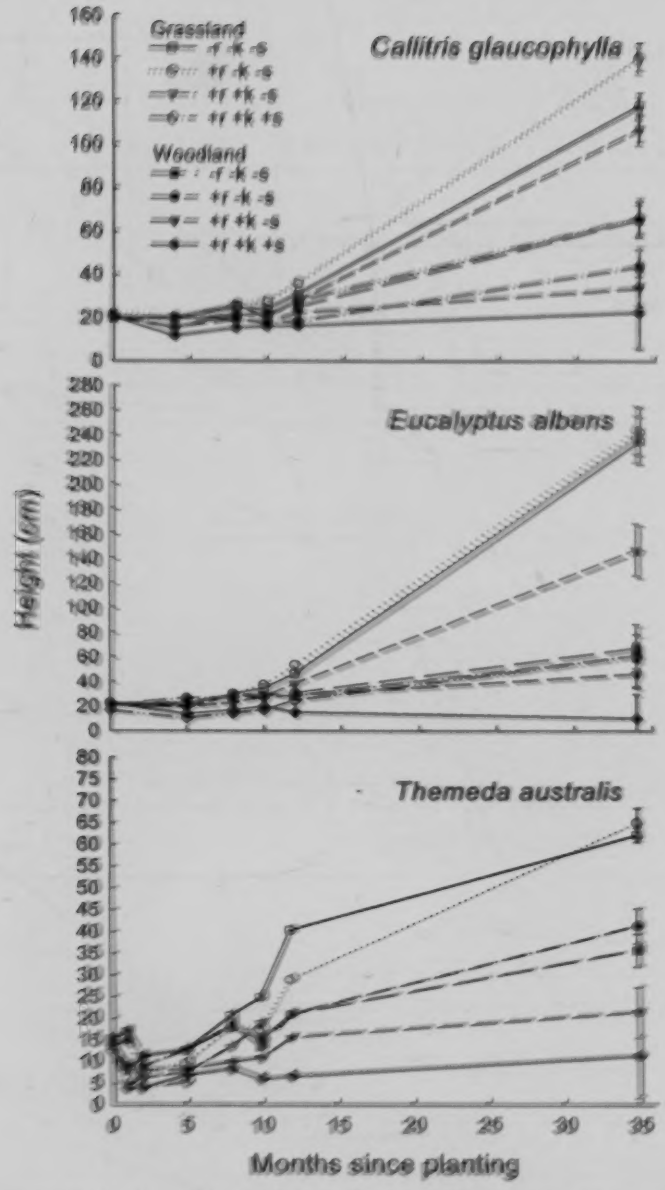


Figure 2.3 Average height of surviving individuals of *Callitris glaucophylla*, *Eucalyptus albens*, and *Themeda australis* in grassland and woodland, under four grazing treatments. Data are weighted averages calculated based on the number of surviving individuals in each of four replicates for each habitat-treatment combination. Error bars are one standard error, and have been omitted from all but the final height measures for clarity.

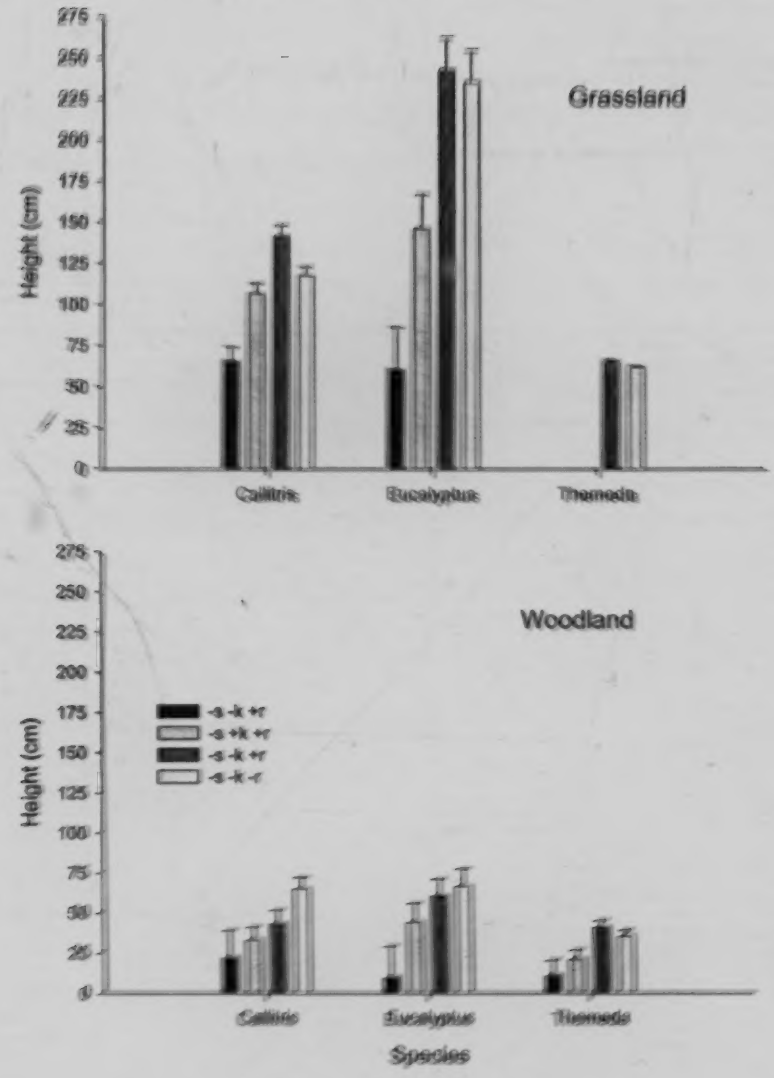


Figure 2.4: Height (± S.E.) of surviving individuals of *Callitris glaucophylla*, *Eucalyptus albens*, and *Themeda australis* in grassland and woodland, after three years in four grazing treatments. Data are weighted averages calculated based on the number of surviving individuals in each of four replicates for each habitat-treatment combination.

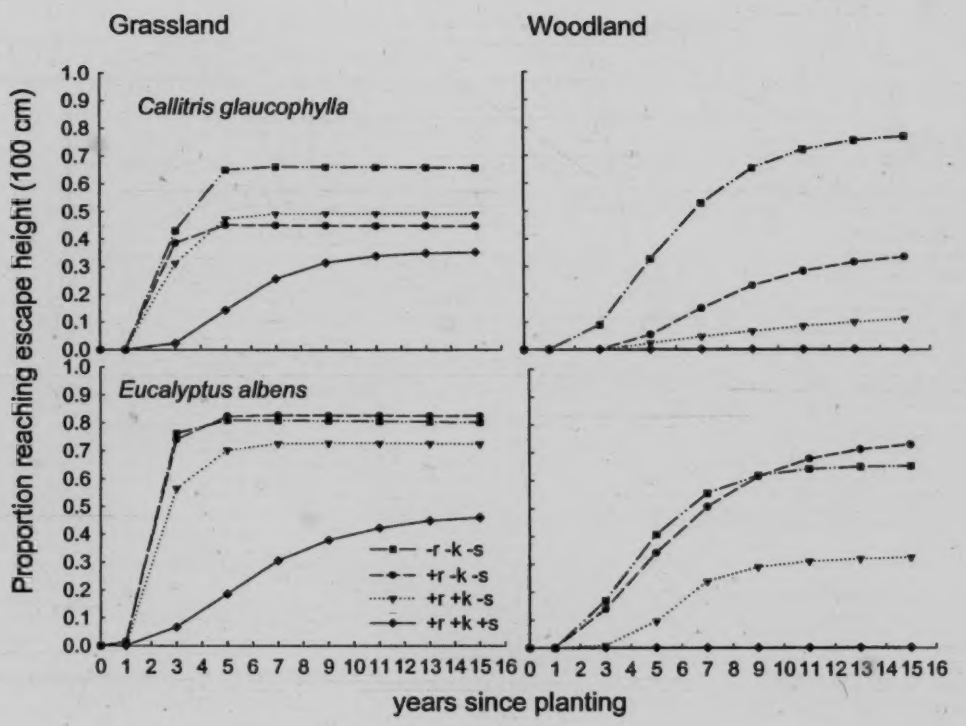


Figure 2.5: Proportions of a cohort of 25cm tall *Callitris glaucophylla* and *Eucalyptus albens* seedlings predicted to reach escape height (>100 cm) after 15 years under four grazing treatments in two habitats. Predictions were based on stage-classified matrix models built for each habitat/species/treatment combination, and transition probabilities were calculated from observed growth and survival rates of seedlings.

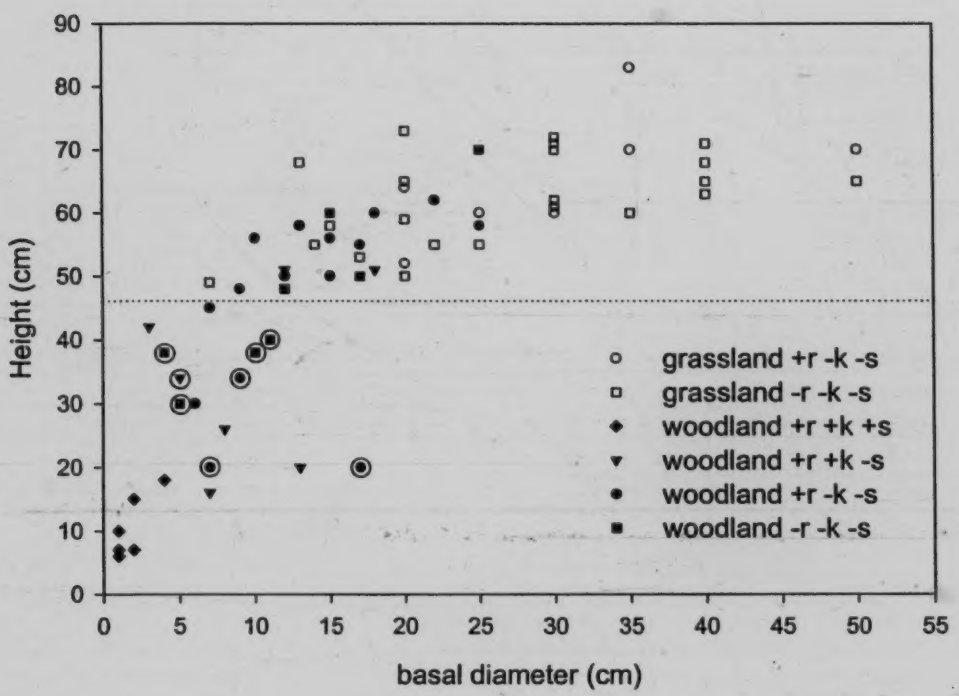


Figure 2.6 Leaf height versus tussock diameter for *Themeda australis* plants surviving to the end of the transplant experiment (April 2001). All plants greater than 45cm in height (dotted line) flowered by the end of the experiment. Individuals that flowered while less than 45 cm in height are circled.

Chapter 3

The effects of phosphorus on growth and competitive interactions of native and introduced species in White Box woodlands[1]

Introduction

Invasion of exotic plant species is a conservation concern in many ecosystems worldwide (Heywood 1989, Hobbs and Humphries 1994). In temperate Australian woodlands, which are among Australia's most poorly conserved and highly modified ecosystems (Benson 1991, Hobbs and Yates 2000a), exotic species are considered a major threat to conservation (Yates and Hobbs 1997, Hobbs and Yates 2000b, Sivertsen and Clarke 2000). There is considerable evidence, both from Australia and worldwide, that exotic species can have a detrimental effect on temperate woodland and grassland ecosystems. In California, introduced annual grasses may impede re-establishment of native perennial grasses (Brown and Rice 2000) and prevent recruitment of sagebrush (Eliason and Allen 1997). In the *Eucalyptus* woodlands of southwestern Australia, exotic species may displace native herbaceous species (Humphries *et al.* 1994, Abensperg-Traun *et al.* 1998) or form dense swards that prevent recruitment of perennial woody species (Hobbs and Atkins 1991). In eastern Australian woodlands, Cluff and Semple (1994) found recruitment of *Eucalyptus* was greater in native than exotic pastures.

The persistence of introduced species has been attributed both to human-related disturbance (Hobbs and Huenneke 1992, McIntire and Lavorel 1994) and to elevated soil nutrient levels (Moore 1970, Hobbs and Atkins 1988, Vinton and Burke 1995). Nutrient enrichment, particularly addition of phosphorus, may encourage invasion and dominance

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of exotic plant species in grassy ecosystems in Australia (Hobbs and Atkins 1988, Morgan 1998, King and Buckney 2000). Australian soils are typically very low in phosphorus, and phosphorus addition (often topdressing with superphosphate fertilizer) is frequently used to improve productivity of pasture. The extent of exotic species invasion of road verges in Western Australia is related to the degree of phosphorus enrichment (Cale and Hobbs 1991). Exotic species richness and cover in remnant grassland in Victoria are strongly correlated with soil phosphorus but not with concentrations of other nutrients (Morgan 1998). O'Dwyer and Attiwill (1999) reported that the exotic grass *Lolium perenne* L. responded more strongly to added phosphorus than the native perennial grass *Austrodanthonia eriantha* (Lindl.) H. P. Linder, and showed enhanced competitive effect under phosphorus enrichment. In addition, research in disturbed White Box (*Eucalyptus albens* Benth.) woodland on the Central West Slopes of New South Wales has shown that exotic species are more abundant in patches with elevated soil phosphorus and nitrogen (Chapter 6) and that exclusion of herbivores does not allow regeneration of native understory when there is a large exotic component to the flora (Allcock *et al.* 1999, Chapter 6).

Rates of growth and resource consumption may differ among species across a resource gradient, and may subsequently affect competition between species (Tilman 1988). If phosphorus enrichment facilitates the invasion of exotic species by stimulating their growth to a greater extent than native species, differential growth responses among White Box woodland species would indicate that phosphorus could facilitate invasion in this ecosystem. If adding phosphorus also increases the competitive effect of exotic species on native species, enrichment could exacerbate the negative effects of exotic species as

well as facilitating their invasion into remnant woodlands. Two glasshouse experiments were designed to test the following three questions relating to the response of White Box woodland species (both native and exotic) to phosphorus:

1. Do exotic and native species show different patterns of growth along a gradient of increasing phosphorus?
2. Do exotic species have a greater competitive effect on native species than do conspecifics?
3. Does phosphorus enrichment compound the competitive effect of exotic species on native species?

The focal species chosen were either important components of box woodland (native grasses and *Eucalyptus albens*) or were common invaders in disturbed box woodlands (exotic speices). Experiment one tested the effect of phosphorus enrichment on the growth of an annual exotic grass (*Vulpia bromoides* (L.) Gray), an annual exotic forb (*Echium plantagineum* L.), three native perennial grasses (*Themeda australis, Bothriochloa macra* and *Austrodanthonia racemosa* (R. Br.) H. P. Linder), and the dominant canopy species, *Eucalyptus albens*. Experiment two investigated the potential for phosphorus enrichment to increase the competitive effect of *Echium plantagineum* and *V. bromoides* on *Eucalyptus albens* and *B. macra.*

Methods

Experiments were conducted from April 2000 to October 2000 in a temperature-controlled glasshouse at the University of Alberta, Edmonton, Alberta, Canada. Glasshouse temperatures ranged from 21° C at night to 28° C during the day (mean

maximum summer temperature in central western NSW is around 29-33° C), and day length ranged from 18 h in mid-summer to 10 h in autumn. Seeds of *T. australis, Eucalyptus albens, A. racemosa,* and *B. macra* were obtained from commercial suppliers who collected the seed from central western NSW, *Echium plantagineum* was collected in the Australian Capital Territory, and *V. bromoides* was provided by the Cooperative Research Centre for Weed Management Systems in Orange, NSW.

Germination and planting

Seeds were germinated in the dark at room temperature in sterile 100 mm petri dishes lined with moistened filter paper. After seedlings had grown in petri dishes for five days, they were transferred into 10 cm diameter free-draining plastic pots containing a 1:1 mixture of sterile potting mix and sterile sand. Seedlings were then watered well and placed in the glasshouse for one week to allow establishment before nutrient treatments were applied. In both experiments, the positions of pots were randomized within an area of 6 m^2 after nutrient treatments were applied, and pots were shifted to new random positions every three weeks. Pots were watered every two days.

Experiment one: response to phosphorus fertilization

Experiment one began on April 19, 2000. Individual seedlings were grown alone in 10 cm pots with one of six levels of available phosphorus (applied as dissolved P_2O_5): 0 parts per million (ppm), 5 ppm, 10 ppm, 15 ppm, 30 ppm and 60 ppm. These levels were chosen to reflect the range of soil phosphorus available in typical disturbed white box woodland (Chapters 5 and 6). One hundred ppm nitrogen (applied as dissolved

NH_4NO_3) was supplied for all treatments. Available phosphorus and nitrogen concentration in surface soil are around 15 p.p.m. and 50 p.p.m. respectively in less disturbed remnants; in degraded remnants available P and N concentrations are around 70 p.p.m. and 90 p.p.m. respectively (Chapter 6). Dissolved nitrogen and phosphorus were added in two doses applied two weeks apart to achieve the total concentrations desired. Eight individuals each of *Eucalyptus albens, B. macra, A. racemosa, Echium plantagineum* and *V. bromoides* were subjected to each level of phosphorus. There were seven replicates of each treatment for *T. australis* due to poor germination. Plants were harvested on June 19, 2000. Shoots were cut off at the soil surface, and roots were removed from the soil using a 3 mm sieve, and then washed in a water bath using forceps to remove debris. Roots and shoots were dried for 48 h at 80°C and then weighed.

Differences in dry weight between species and nutrient levels were analyzed using a generalized least squares regression model (S-Plus 2000 function gls, MathSoft Inc. 1999) including a species-nutrient interaction. Variances were estimated separately for each species. Separate analyses were performed for root and shoot biomass.

Experiment two: competition/fertilizer interactions

Experiment two began August 29, 2000 and was harvested October 13, 2000. The experiment was designed to test the competitive effect (the degree to which a species suppresses growth of a target plant: Goldberg and Fleetwood 1987) of *V. bromoides, Echium plantagineum* and conspecific individuals on *Eucalyptus albens* and *B. macra* at two concentrations of soil phosphorus. Seedlings of *Eucalyptus albens* and *B. macra* were either grown alone, with another individual of the same species, or with an

individual of an exotic species (*V. bromoides* or *Echium plantagineum*). Each pot received either 10 ppm or 100 ppm phosphorus added as dissolved P_2O_5, and 100 ppm nitrogen was added as dissolved NH_4NO_3. Nutrients were added in three doses one week apart. There were twelve replicates of each competitive treatment (conspecific, *V. bromoides* and *Echium plantagineum*) for each native species at each phosphorus level, and six single plants of each native species at each nutrient level. Again, shoots were cut off at the soil surface and dried for 48 h at 80°C. Roots could not be processed immediately due to logistic limitations, and were stored at 4°C from October 13 to December 5 after which they were removed from the soil as in experiment one and dried for 48 h at 80°C.

Two-way ANOVA (S-Plus 2000 function aov, MathSoft Inc. 1999) was used to compare the final dry weights. Separate analyses were performed for *B. macra* and *Eucalyptus* shoots and roots. In each case, the response variable was dry shoot or root biomass of the native species, and in the treatments with a conspecific competitor one of the two individuals was chosen randomly and sampled as the target plant. Phosphorus level (10 ppm or 100 ppm) and species of competitor (none, conspecific, *V. bromoides* or *Echium plantagineum*) were the factors. Data required log-transformation to ensure homogeneity of variances (Sokal and Rohlf 1981).

Results

Experiment one

The six species tested differed both in their final biomass and in their response to phosphorus fertilization (Figs. 3.1, 3.2). *Echium plantagineum* individuals were the

largest plants at the end of the experiment, and showed a strong positive response to added phosphorus in both shoot and root biomass. *Vulpia bromoides* plants were also generally larger than individuals of the four native species used and showed a positive response in shoot and root biomass with increasing phosphorus. Both exotic species, *Echium plantagineum* in particular, showed a greater increase in growth with additional phosphorus than did the native species (Figs. 3.1, 3.2, 3.3).

Generalized least squares regressions indicated that both species and phosphorus concentration were important predictors of final shoot biomass (species: $F=142.62$, $df=5$, $p < 0.0001$; phosphorus: $F=25.8$, $df=1$, $p<0.0001$). There was a highly significant interaction between species and phosphorus concentration ($F=28$, $df=5$, $p < 0.0001$). Results for root biomass were very similar. Species identity and phosphorus concentration were again very important predictors (species: $F=59.01$, $df=5$, $p < 0.0001$; phosphorus: $F=28.35$, $df=1$, $p<0.0001$) and there was a significant interaction ($F=10.9$, $df=5$, $p < 0.0001$). Figure 3.3 shows parameter estimates and 95% confidence intervals for the shoot (Fig. 3.3a) and root (Fig. 3.3b) responses to phosphorus treatments for each species (i.e. the slopes of the relationships illustrated in Figs 3.1 and 3.2). None of the three native grass species showed a significant response to phosphorus addition. *Eucalyptus albens* shoots showed a slight significant positive response. *Vulpia bromoides* shoots showed a significantly greater response than *B. macra* and *T. australis*. The response of *Echium plantagineum* shoots was greater than that for all other species. Root biomass response to phosphorus showed a similar pattern. No native species showed a significant response, roots of *V. bromoides* showed a significant positive

response, and *Echium plantagineum* roots showed the strongest positive response to phosphorus addition.

Experiment two

Some of the pots in experiment two incurred fungal infection resulting in mortality of individual plants early in the study, reducing the number of replicates of each treatment. Mortality of *Echium plantagineum* was so great that the *B. macra* versus *Echium plantagineum* treatment was discarded, resulting in three treatments for *B. macra*: no competitor, conspecific competitor and *V. bromoides* competitor. A few root samples were damaged during storage and were discarded; therefore sample sizes used in analyses of root biomass were smaller than those for shoot biomass.

For *Eucalyptus albens*, both competitive treatment and addition of phosphorus had a significant effect on shoot biomass (log-transformed) at the end of the experiment (Table 3.1, Fig. 3.4a). Plants grown with *Echium plantagineum* were significantly smaller at both phosphorus levels than plants in any other treatment. The *V. bromoides* treatment produced shoot biomass significantly lower than the "no competitor" treatment. Plants in the high phosphorus treatment produced significantly more shoot biomass than those in the low phosphorus treatment, but there was no significant interaction with species of competitor. Root biomass of *Eucalyptus albens* showed a similar response to shoot biomass (Fig. 3.4b). Both phosphorus treatment and species of competitor were significant in the ANOVA model (Table 3.1), and there was no significant interaction between phosphorus level and competitor. In *a posteriori* comparisons there were significant differences in root weight between the *Echium plantagineum* treatment and all other competitive treatments, and a significant difference between the *V. bromoides*

treatment and the no competitor treatment. Indices of the competitive effect of conspecifics and both exotic species are given in Table 3.3.

For *B. macra*, addition of phosphorus resulted in significantly greater shoot biomass at the end of the experiment, but competitive treatment had no effect (Table 3.2), and there was no interaction between competitive treatment and phosphorus level (Fig. 3.5a). Similarly for *B. macra* root biomass only phosphorus level was significant in the ANOVA model, with no effect of competitive species and no interaction (Table 3.2, Fig. 3.5b). The competitive effects of *V. bromoides* and *B. macra* were minimal at both phosphorus levels (Table 3.3).

Discussion

These experiments support the hypothesis that phosphorus enrichment could give an advantage to exotic species in grassy White Box woodlands. Both exotic species tested, particularly *Echium plantagineum*, showed a greater response to phosphorus addition in the first eight weeks of growth than did any of the native species; indeed, several native species showed no response at all. O'Dwyer and Attiwill (1999) found a similar result in their experiments with *Austrodanthonia eriantha* and *Lolium* sp. They also found that *Lolium* was able to suppress growth of *A. eriantha* to a greater extent under phosphorus enrichment, and concluded that this interaction may have facilitated the reduction of *A. eriantha* cover where soil phosphorus was greater than 14 ppm. The experiments presented here showed no interaction between competitive effect and phosphorus concentration in the first eight weeks of growth; however phosphorus addition could still facilitate recruitment of exotics into woodland remnants by stimulating seedling growth

in areas where low phosphorus would normally inhibit growth of exotic species. Phosphorus enrichment could also result in dominance of exotic species by encouraging their early growth to a greater extent than native perennial species resulting in increased competition for space and light later on, particularly when exotic species are present at high density.

Shoot biomass of *V. bromoides* and *Echium plantagineum* showed a stronger response to phosphorus addition than root biomass (although very fine roots were not measured). While studies have attributed the negative effects of exotic annual species on perennial species to competition for soil resources (for example, nutrients: O'Dwyer and Attiwill 1999; water: Eliason and Allen 1997), the negative effect of exotic species is likely via competition for light and space as well as competition for soil resources. Physical overgrowth and crowding may lead to mortality of tree seedlings and perennial grass tussocks (Chapter 2), and sward formation may prevent recruitment of some native species (Hobbs *et al.* 1988, Windsor 1998, 2000).

While the competitive effect of individual plants of *Echium plantagineum* and *V. bromoides* was not altered by nutrient addition, it was generally greater than the competitive effect of a conspecific competitor, and this result was consistent for both shoot and root biomass. *Echium plantagineum* showed a much stronger effect than *V. bromoides* in these experiments, indicating that *Echium plantagineum* might be a more noxious species in invaded remnant vegetation. However, in a field experiment conducted between April 1998 and April 1999, overgrowth by a sward of *V. bromoides* (and other annual exotic grasses) after grazing ceased was an important cause of mortality for planted *Eucalyptus albens* and *T. australis* seedlings (Chapter 2), and *Vulpia* spp.

seeds can be extremely abundant in the seed bank of disturbed woodland (Board 2002). The negative effect of *V. bromoides* and other annual grasses might be related to formation of dense swards that overgrow slower growing perennial plants thus preventing recruitment of native seedlings (as in Hobbs and Atkins 1991), or increase competition for soil resources such as moisture (Gordon and Rice 1993).

Once annual exotic species are established, they may be able to prevent re-establishment of native species, because they differ in their effects on nutrient cycling. Nutrients may cycle at different rates and vary seasonally in communities dominated by species with different life histories (Whitford and Herrick 1995). Annual exotic species could potentially maintain high-nutrient patches with rapid nutrient turnover, and these patches would favor re-establishment of the annual species. This feedback has been demonstrated in Colorado steppe grasslands (Vinton and Burke 1995), where an exotic annual grass invaded patches that were enriched with nitrogen. These patches were still dominated by the annual grass, and maintained high nitrogen levels, twenty years after a single fertilization event. Soil phosphorus has low mobility (Russell 1961) and would also likely maintain a high stable concentration in enriched patches. Much of this phosphorus would be inaccessible to plants, however, and field experiments testing the potential for phosphorus to create feedbacks leading to annual plant dominance should be performed.

The results presented here show that growth of exotic species is stimulated by phosphorus addition in a controlled glasshouse experiment, but it is difficult to extrapolate from such a small scale and short term study to the effects of phosphorus enrichment in the field. Longer-term studies of the effects of phosphorus enrichment and

field experiments in remnant white box woodlands are necessary, as are investigations of competitive interactions between native species. Plant density, concentrations of nitrogen or other nutrients, the presence of vesicular-arbuscular mycorrhyzae (VAM), and the effects of grazing or fire disturbance could mediate the effects of phosphorus addition in the field, and should be investigated.

Current evidence suggests a high potential for phosphorus enrichment to facilitate invasion in White Box woodland. Exotic species, particularly the two tested in this study, are often at high density in remnant White Box woodlands. Nitrogen is unlikely to be limiting in phosphorus-enriched areas because nitrogen and phosphorus enrichment often coincide either because of animal activity (stock camps) or because of sowing of non-native clovers into native pastures that have been top-dressed with superphosphate (e.g. Donald and Williams 1954; Chapter 6). Addition of phosphorus generally reduces the degree of VAM infection in roots (Richards 1987), and inoculation with mycorrhizae has been found to increase growth only at low levels of available phosphorus for both pasture grasses (Armstrong *et al.* 1992) and *Eucalyptus* seedlings (Chen *et al.* 2000), therefore the presence of VAM is unlikely to advantage native species in elevated phosphorus conditions. Fire or grazing would open space for seedling recruitment, and this study shows that phosphorus addition stimulates early growth of exotic species to a greater extent than native species in White Box woodland. As a result, the interaction between disturbance and phosphorus addition would likely increase the degree of exotic invasion because exotic seedlings would grow faster and take over any gaps created by the disturbance.

Several studies have indicated a relationship between grazing intensity and degree of invasion in grassy woodland systems (Prober and Thiele 1995, Abensperg-traun *et al.* 1998), and removal of stock is a common restoration technique in such ecosystems (e.g. Elix and Lambert 1997). However, the strong response of some exotic species to available nutrients, the formation of swards favoring their re-establishment while inhibiting establishment of native perennial species, and the differences in nutrient cycling between annual- and perennial- dominated patches may create a feedback and allow exotic species usually associated with disturbance to persist in high-nutrient patches even when stock grazing is removed. Understanding of the effects of nutrient enrichment on exotic species invasion in grassy White Box remnants, and the potential interactions with disturbance, is necessary for designing effective conservation and restoration plans.

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Table 3.1: Results of two-way ANOVA of *Eucalyptus albens* shoot and root dry weight (log-transformed) with P treatment and species of competitor as factors.

Shoots	DF	SS	MS	F	P
Competitor	3	19.85	6.55	18.77	<0.0001
P	1	1.98	1.98	5.62	0.021
Competitor x P	3	0.91	0.30	0.86	0.46
Residual	63	22.2	0.36		
Roots					
Competitor	3	10.56	3.52	11.72	<0.0001
P	1	2.04	2.04	6.79	0.012
Competitor x P	3	0.20	0.07	0.22	0.88
Residual	53	15.92	0.30		

Table 3.2: Results of two-way ANOVA of *Bothriochloa macra* shoot and root dry weight (log-transformed) with P treatment and species of competitor as factors.

Shoots	DF	SS	MS	F	P
Competitor	2	3.56	1.77	1.84	0.17
P	1	24.38	24.38	25.25	<0.0001
Competitor x P	2	0.30	0.15	0.16	0.86
Residual	47	45.37	0.97		
Roots					
Competitor	2	0.015	0.007	0.015	0.98
P	1	6.95	6.95	16.03	0.0002
Competitor x P	2	0.64	0.32	0.74	0.48
Residual	43	18.64	0.43		

Table 3.3: Competitive effect calculated as (dry weight native alone – dry weight native with competitor)/dry weight native alone for conspecifics, *Echium plantagineum* and *Vulpia bromoides* on *Eucalyptus albens* and *Bothriochloa macra*. Values in parentheses are standard error.

a) 10 ppm Phosphorus	*Eucalyptus albens*		*Bothriochloa macra*	
Competitor	**Shoots**	**Roots**	**Shoots**	**Roots**
Eucalyptus albens	0.001 (0.11)	0.35 (0.07)	-	-
Echium plantagineum	0.65 (0.09)	0.68 (0.08)	-	-
Vulpia bromoides	0.06 (0.09)	0.54 (0.05)	0.22 (0.34)	0.15 (0.21)
Bothriochloa macra	-	-	-0.26 (0.31)	-0.05 (0.16)

b) 100 ppm Phosphorus	*Eucalyptus albens*		*Bothriochloa macra*	
Competitor	**Shoots**	**Roots**	**Shoots**	**Roots**
Eucalyptus albens	0.0003 (0.14)	0.33 (0.09)	-	-
Echium plantagineum	0.64 (0.08)	0.73 (0.07)	-	-
Vulpia bromoides	0.32 (0.12)	0.44 (0.17)	0.07 (0.25)	-0.23 (0.24)
Bothriochloa macra	-	-	-0.08 (0.16)	0.06 (0.14)

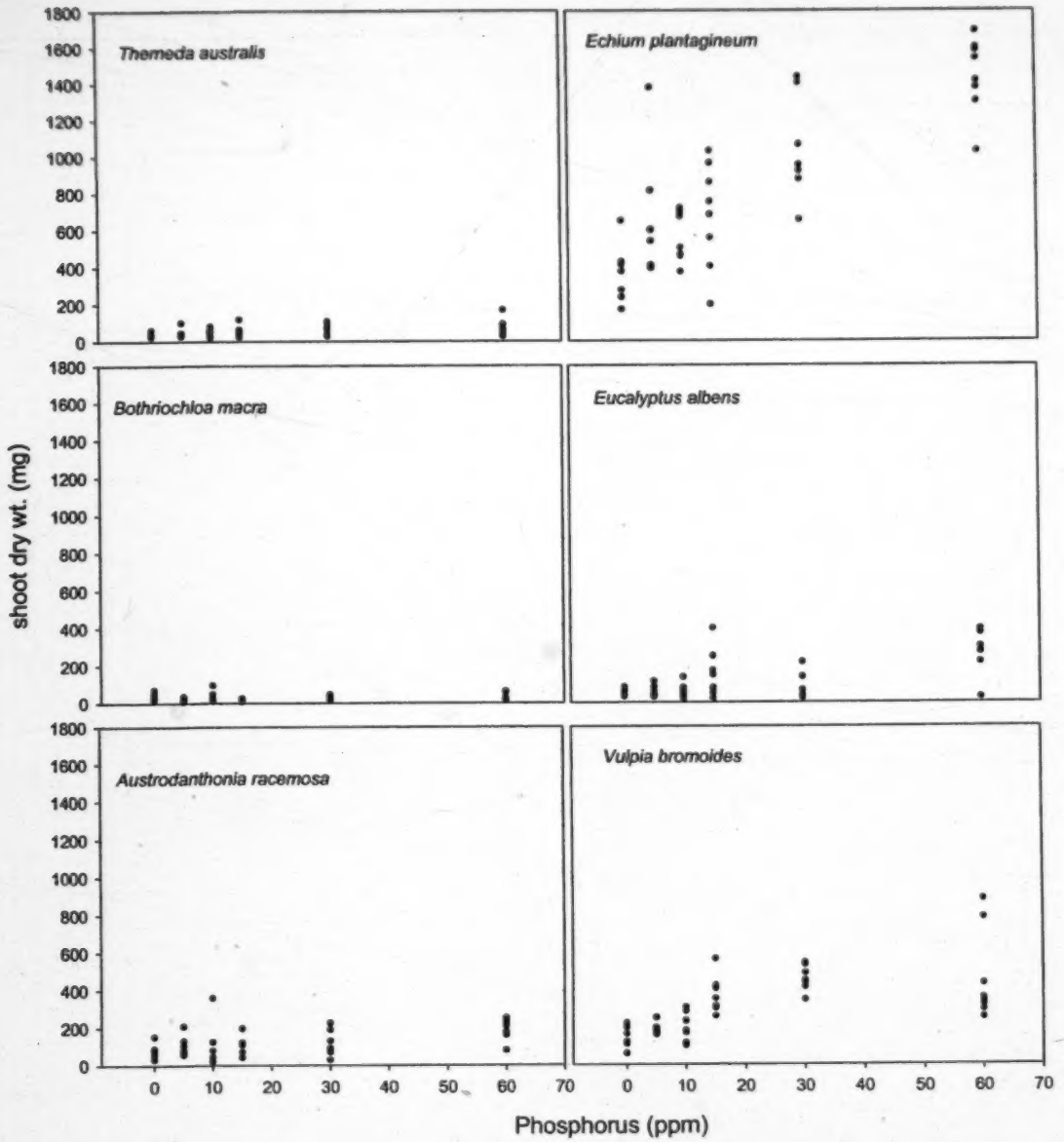

Figure 3.1: Shoot dry weights of four native and two exotic White Box woodland species, grown under six levels of available phosphorus. *N*=8 for all species and phosphorus concentrations except for *T. australis* for which *N*=7.

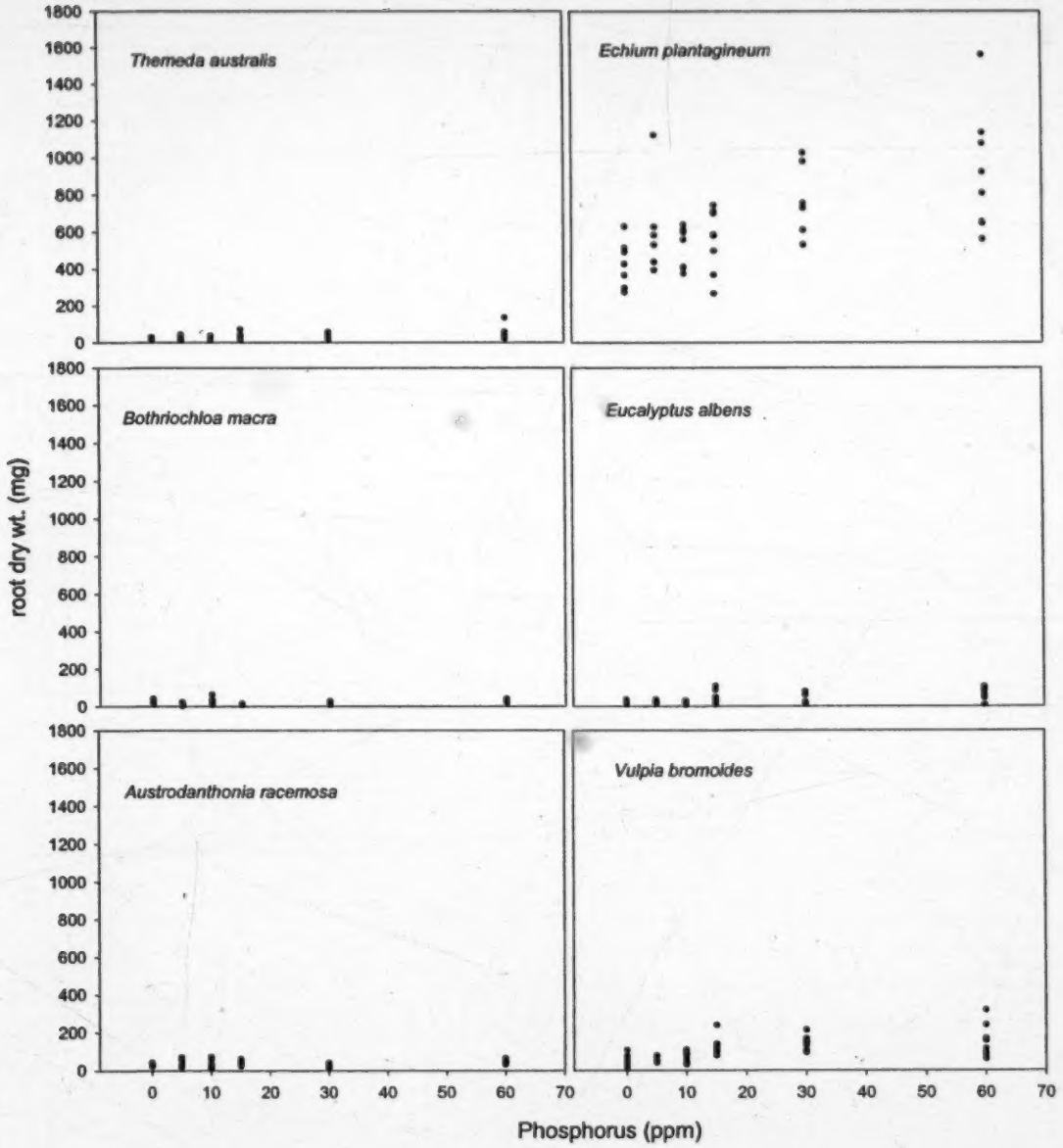

Figure 3.2: Root dry weights of four native and two exotic White Box woodland species, grown under six levels of available phosphorus. *N*=8 for all species and phosphorus concentrations except for *T. australis* for which *N*=7.

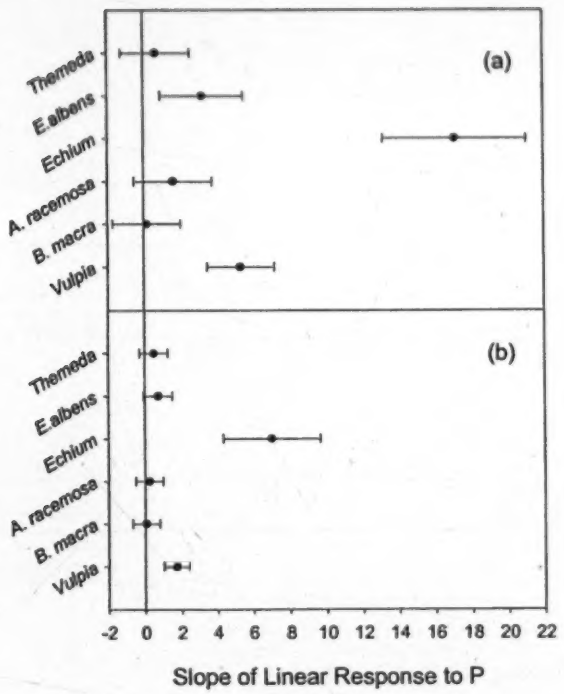

Figure 3.3: Parameter estimates (the slope of the relationship between biomass and phosphorus concentration) and 95% CI's for the response of shoot biomass (a) and root biomass (b) to changes in phosphorus concentration for *T. australis, B. macra, A. racemosa, Echium plantagineum, Eucalyptus albens,* and *V. bromoides.*

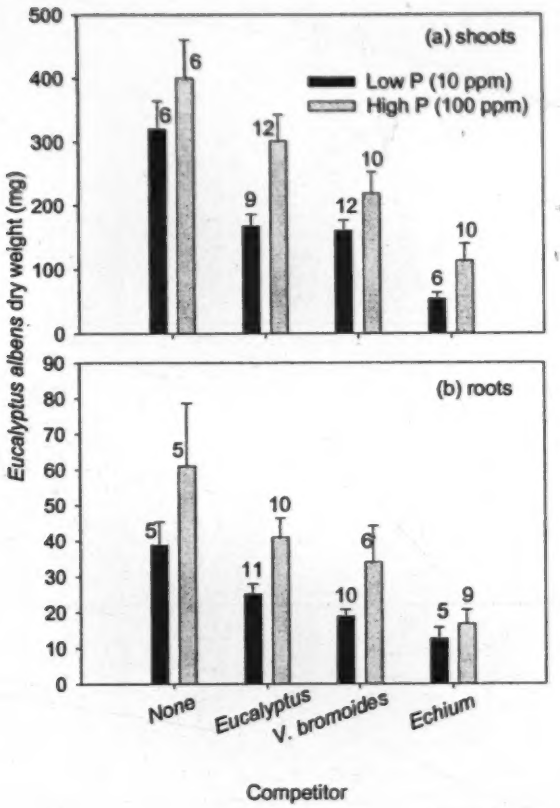

Figure 3.4: Mean shoot (a) and root (b) dry weight for *Eucalyptus albens* seedlings (±S.E.) in four competition treatments (no competitor, conspecific competitor, *Vulpia bromoides* competitor, or *Echium plantagineum* competitor) grown under two levels of available phosphorus. Numbers indicate sample size.

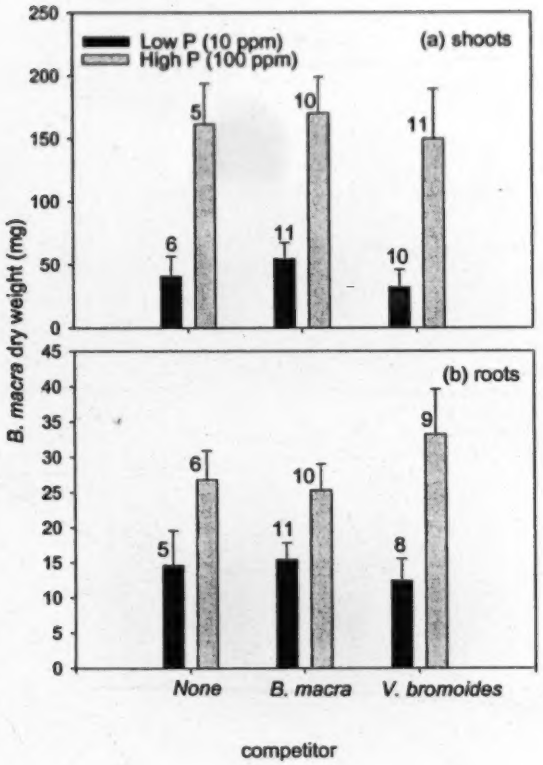

Figure 3.5: Mean shoot (a) and root (b) dry weight for *Bothriochloa macra* seedlings (±S.E.) in three competition treatments (no competitor, conspecific competitor, or *Vulpia bromoides* competitor) grown under two levels of available phosphorus. Numbers indicate sample size.

Chapter 4

What determines disturbance-productivity-diversity relationships? The effects of scale, species, and environment on richness patterns in an Australian woodland[1]

Introduction

A clear understanding of the relationships between disturbance and diversity (Connell 1978, Petraitis *et al.* 1989, Mackey and Currie 2001, White and Jentsch 2001), and productivity and diversity (Grime 1973, Waide *et al.* 1999, Mittelbach *et al.* 2001) remains elusive, and published studies have reported numerous patterns. There is an emerging consensus that much of the variation can be explained by potentially confounding effects of scale (Wardle 1999, Weiher 1999, Safford *et al.* 2001, Chase and Leibold 2002) and species identity (Aarssen 1997, Loreau 2000, Adler and Bradford 2002). A wide variety of factors influence species coexistence, and changing these will alter the shape of the diversity-productivity or diversity-disturbance relationship (e.g. Huston 1979, Tilman 1999, Chesson 2000, Cardinale *et al.* 2000). For example, Mouquet *et al.* (2002) have recently shown using simulation models that the specific mechanism contributing to species coexistence (e.g. size of the regional species pool, recruitment limitation, or heterogeneity) can determine the relationship between diversity and productivity.

The processes invoked as mechanisms for determining hump-shaped diversity-productivity-disturbance relationships (recruitment, individual survival, competitive exclusion, or space pre-emption) operate at small spatial scales, on the order of cm^2 or m^2 for herbaceous plant communities. However, other factors affecting diversity, notably

[1] Manuscript in review at *Oikos*.

the species pool, may operate at much larger spatial scales (e.g. Zobel 1992). Studies conducted at larger spatial scales have found monotonic increases in diversity with productivity (Chase and Liebold 2002) or no relationship between disturbance and diversity (Stohlgren *et al.* 1999). At a community or regional scale competitive exclusion, space pre-emption and recruitment of individuals may be less important than availability and dispersal of species from the species pool (Zobel 1992, Huston 1999).

In Australian temperate woodlands, patterns of disturbance and productivity have changed considerably since European settlement two hundred years ago (Sivertsen and Clarke 2000). White Box woodlands in south-eastern Australia have been reduced to 0.01% of their original extent (Prober and Thiele 1993), and remnants are often heavily grazed by livestock, macropods, and rabbits. In areas where trees were cleared, phosphorus fertilizer and non-native legumes were frequently added to increase pasture productivity. In addition, numerous exotic plant species (often European or Mediterranean in origin) were introduced and have invaded many remnants. The resulting landscape is a mosaic consisting of treed remnants of moderate to low fertility, intermediately to highly productive mixed pasture and alluvial run-on zones, and highly modified cropland and exotic pasture. Most of the native species in this system are perennial grasses and forbs, while most of the exotic species are fast-growing annuals. This difference in species characteristics may result in different species richness patterns in response to changes in disturbance and productivity, and has been observed in other woodland communities (McIntyre and Lavorel 1994, Harrison 1999).

Herbivory is currently the primary disturbance in white box woodland, especially since fire regimes have changed with European settlement. Native, domestic, and feral

herbivores can remove substantial biomass and have the potential to limit plant recruitment or alter community structure (Short 1985, McIntyre and Lavorel 1994, Prober and Thiele 1995).

Our study used a series of herbivore exclusion fences placed in remnant white box woodland, cleared grassland, and alluvia to assess the response of vegetation to changes in herbivory in habitats that differed in productivity. Four fencing treatments were used to selectively exclude herbivores of different body sizes, creating a gradient of grazing disturbance. We used species richness as our measure of diversity, and sampled richness at 1 m^2 and 625 m^2 (25m by 25m) scales. We also measured standing crop at 625m^2 and total vegetation cover at both scales as surrogates for site productivity. We addressed the following questions about the relationship of native, exotic and total species richness to grazing disturbance and standing crop along a productivity gradient.

1. How well do disturbance, productivity (reflected by biomass, cover and habitat) and environmental variables predict species richness at 1 m^2 compared to 625 m^2?

2. What are the shapes of the relationships of richness to biomass, cover, and disturbance level at 1 m^2 compared to 625 m^2?

3. How might species characteristics affect the relationships? Specifically, do native and exotic species show different patterns of diversity in response to disturbance, productivity, and environment?

Methods

Study area

The study was conducted on the eastern foreshores of Burrendong Dam (32° 40' S, 149° 6' E), part of a large catchment area administered by the Department of Land and Water Conservation of New South Wales. The lower slopes of the foreshores, originally dominated by white box (*Eucalyptus albens*) woodlands, were largely cleared of trees in the 1800s to promote pasture growth, although some wooded patches remain. The lower slopes are dissected by drainages containing patches of deep alluvial soil. Sheep and cattle are grazed under license, and there are large numbers of eastern gray kangaroos (*Macropus giganteus*; between 15 and 38 sightings per spotlight kilometer – D. Hik and A. Newsome, unpublished data), wallaroos or euros (*M. robustus*) and swamp wallabies (*Wallabia bicolor*). Rabbit haemorhagic disease (RHD) arrived at Burrendong Dam in the winter of 1996 and reduced the rabbit population substantially (Saunders *et al.* 1998); however, rabbits are still present at relatively high density (5 sightings per spotlight kilometer: D. Hik and A. Newsome, unpublished data).

Experimental and sampling design

In January-February 1997, we constructed a series of 25 m by 25 m (625 m^2) fences to investigate the impact of grazing on understory vegetation in cleared (grassland), white box woodland, and alluvial habitats. The experiment was replicated in four blocks (creek watersheds) separated by 1-3 km. Within each block there were 12 experimental plots, evenly distributed in white box woodland, grassland, and alluvia. Four treatments were applied in each habitat: unfenced, stock fence (excluded sheep and cattle), kangaroo

fence (excluded sheep, cattle and kangaroos), and rabbit fence (excluded sheep, cattle, kangaroos, and rabbits), for a total of 48 experimental plots (see Chapter 1). The design created an herbivory (disturbance) gradient within the context of a productivity gradient (among habitats, with woodlands the least productive and alluvia the most productive). Experimental plots were sampled in summer (February-March 1997, 1998, 1999, 2001), and spring (October 1998, 2000).

In each experimental plot, ten 1 m^2 quadrats were selected for permanent monitoring and the corners were marked with pegs. For each quadrat we identified all plant species present, and estimated total percent cover of all living and dead vegetation (ocular estimate of foliar cover in $1m^2$, dead and live estimated separately). Complete species lists were compiled for each 625 m^2 experimental plot following each quadrat sampling. Finally, species lists for each of the habitats in the entire study area were compiled using information from other ongoing vegetation research (the complete species lists are presented in Appendix 1). Maximum peak live biomass is the most commonly used estimate for net primary productivity in grasslands (Scurlock *et al.* 2002) therefore we used standing biomass as our measure of productivity. To estimate standing biomass (current year's growth: living and recently cured vegetation) at the $625m^2$ scale in each sampling period, we clipped herbaceous vegetation at twelve random points in each experimental plot. At each point, standing herbaceous vegetation rooted within a seven cm diameter circle was clipped at ground level. Samples were bulked to give one biomass estimate per experimental plot, dried for 48 hours at 80^{o} C, and weighed.

Analysis

Repeated measures ANOVAs (SAS procedure MIXED, SAS institute 2000) were conducted on standing biomass and richness data from both the whole plots and the quadrats (nested within experimental plots) to test the effects of the experimental disturbance gradient (Littell *et al.* 1996, Underwood 1997). Because species counts were Poisson-distributed, richness data were log-transformed. As there was a large annual exotic component to the flora, which caused differences in composition and biomass between seasons, we analyzed spring (October) and summer (March) samples separately. Only summer biomass samples were analysed in this way, because the time series contained four sampling periods (compared to two for spring) and trends in biomass accumulation could be observed. For graphical representation of richness with respect to disturbance, an index of disturbance level in each grazing treatment (i.e. position of points on the X axis) was calculated based on the average total cover (sum of living and dead) in summer 2001, and disturbance level was depicted as a continuous variable; however, for statistical analyses disturbance (i.e. fencing treatments) was treated as categorical.

To test the relationship of species richness to disturbance (i.e. fencing treatments), standing crop, cover, and environmental variation we performed a series of log-linked generalized linear models (GLMs) built using a forward stepwise procedure (S-Plus 2000, Mathsoft Inc. 1999). Analyses were performed for overall richness, native species richness and exotic species richness measured at the 625 m^2 (whole plot) and $1m^2$ (quadrat) scales. To ensure that we drew conservative conclusions from the large number

of models, a significance level of p=0.01 for both ANOVA and GLM analyses was adopted.

The following variables were included for model selection: season; habitat; standing biomass; total cover (sum of living and dead vegetation cover averaged across quadrats within each experimental plot); average monthly rainfall in the three months preceding sampling; months since fencing; fencing treatment (disturbance level); the habitat * biomass and habitat * cover interactions; and the treatment * months and treatment * rainfall interactions. Both cover and standing crop were included because cover indicated availability of space for recruitment, while biomass is a commonly used surrogate for productivity (Scurlock *et al.* 2002) and was related to above-ground competition for both light and space. To test whether the relationships between richness and biomass or cover were hump-shaped, we included second order polynomial terms for these two variables. For models of richness at the quadrat level we used the mean richness per 1 m^2 for each experimental plot at each sampling time as the response variable.

Results

Standing biomass

Standing crop in the experimental plots varied annually ($F_{3,34}$ =18.03, p<0.0001), and there were significant effects of both treatment and habitat over time (treatment: $F_{9,82.9}$=4.39, p=0.0001; habitat: $F_{6,68}$=5.98, p<0.0001). Habitats were initially different in biomass (woodlands lowest and alluvia highest). With the exception of March 1998 (12 months since exclosure, Fig. 4.1), woodlands showed a steady increase in summer biomass following removal of grazers, grasslands showed an increase and then a plateau,

and alluvia showed an initial increase in biomass then a decrease in 1999 and 2001 (24 and 48 months since exclosure; Fig. 4.1). Biomass in all habitats and treatments fell dramatically from March 1997 (0 months) to March 1998 (12 months) during a period of below average rainfall (approximately 50% of average from September 1997 to April 1998, 5 to 13 months since exclosure). The degree of biomass reduction was related to the level of disturbance, with unfenced plots showing the greatest decline and complete exclosures the least (Fig. 4.1). Following a drought-breaking rain in May 1998 (14 months since exclosure) alluvia showed the most dramatic biomass increase, followed by grassland, then woodland.

Species richness and scale

Spatial patterns of species richness differed among the three habitats sampled. There were a total of 307 species identified in the study area (see Appendix 1). Alluvia had the smallest species pool, with 160 species, while 207 species were found in grasslands and 191 in woodlands. Woodlands had the largest pool of native species (120) compared to grasslands (114) and alluvia (46). The numbers of exotic species were largest in alluvia (114), followed by grassland (93) and woodland (71). At the 625 m^2 scale, there was little difference in species richness among habitats or treatments prior to the implementation of the disturbance gradient, and all plots contained 30 to 35 species (Fig. 4.2). Quadrat richness (1 m^2) was initially similar in alluvial and grassland habitats (10 species per quadrat) and lower in woodlands (6 or 7 species per quadrat; Fig. 4.2).

Effects of disturbance

Repeated measures ANOVAs indicated that species richness in the experimental plots changed significantly over time at both spatial scales (Table 4.1). However, at the whole plot level there was no significant effect of disturbance level (treatment) over time in either season for any of the species groups, with the exception of exotic species in summer samples. There was a significant year by habitat interaction in summer for all species groups indicating that different habitats responded differently over time at the whole plot level (Table 4.1).

At the quadrat level, there were significant effects of treatment over time for all seasons and species groups with the exception of native species in spring. There were also significant year by habitat interactions as for the whole plot analysis. In addition, there was a significant three-way interaction between year, habitat, and disturbance (treatment) showing that at the quadrat level the different habitats responded differently to disturbance over time.

Although there were changes in richness with both disturbance and time in all habitats, the response of richness to disturbance over time was inconsistent. Most predicted patterns of richness and disturbance were observed from year to year and season to season (Fig. 4.2). Season had the strongest effect on species richness, with much greater total and exotic richness in spring than in summer, while the seasonal difference in native richness was generally smaller. Because the study encompassed unusually dry, unusually wet, and average rainfall years, the effect of rainfall was also marked. During drought (summer 1998) there was generally a linear decline in richness with increasing disturbance, but in wet years (spring and summer 1999), there was linear increase in

richness with increasing disturbance, especially for exotic species in more productive habitats. In general, native species richness showed little effect of disturbance in any habitat or year, with the exception of 1998 where native richness generally declined with disturbance (Fig. 4.2).

The patterns of richness in relation to disturbance were similar at both spatial scales, though the variability in richness at the quadrat level was lower. There was little evidence for a hump-shaped relationship between richness and disturbance level in any habitat, year, or season. Total species richness in woodlands in final year of sampling showed a tendency towards greater richness at intermediate disturbance at both spatial scales, as did exotic species richness in grasslands in 1999 and 2001 (Figure 4.2). However, there was certainly no strong trend towards unimodal richness-disturbance relationships, this did not change with spatial scale, and the richness-disturbance relationship was highly dependent on annual variability in rainfall, vegetation seasonality, and the origin of the plant species.

Predictors of species richness: Generalized Linear Models (GLM)

The first predictor variables to be selected for the GLMs at both scales were usually related to environmental conditions (Table 4.2). At the plot level, season explained over 30 percent of the variation in total species richness and almost 58 % of variation in exotic species richness (greater richness in spring than in summer in both cases). Season was not a significant contributor to variation in native richness at the whole plot scale, and habitat was the best predictor (Table 4.2). At the quadrat level, average rainfall explained 55% of variation in total species richness (increasing richness with increasing rainfall)

but was a much less significant predictor for either native or exotic richness. Variation in exotic species richness was again primarily related to season at the quadrat scale. Native species richness was not related to season at the quadrat level, and habitat was the best predictor of native richness (Table 4.2).

The next best predictor variables in models of both quadrat and whole plot richness tended to be our surrogates for productivity (average cover, standing biomass, or habitat) and deviance explained was generally much lower than for the first variables selected (Table 4.2). Habitat and average cover were the next additions to the model of overall species richness at the whole plot level. Cover was selected second for the models of both native and exotic richness at the whole plot level. Cover was also the second most important predictor of native and exotic richness at the quadrat scale, and biomass was the second most important predictor of total species richness at the quadrat scale. In all models both cover and biomass were selected as significant predictors of species richness, although they were correlated ($r=0.53$).

In almost all models at both spatial scales, a quadratic representation of either cover or standing biomass fit significantly better than a linear representation. Exceptions to this were a significant positive linear relationship of exotic richness to biomass at the whole plot level, and a significant negative linear relationship of native richness to biomass at the quadrat level. In cases where the relationship was polynomial, the second term had a negative coefficient, indicating a hump-shaped relationship between richness and cover or biomass (Table 4.2, Figs 4.3 and 4.4). The strength of the relationship between productivity variables and diversity did not differ greatly between the 625 m^2 and the 1

m^2 sampling scales, but the degree of curvature (indicated by the size of the second order coefficient) was generally greater at the 1 m^2 scale (Table 4.2).

While the response of species richness to cover or biomass appeared to be generally unimodal at both spatial scales, native species and exotic species showed opposing responses. At both scales, native richness tended to decline with average cover and standing biomass (Table 4.2, Figs 4.3 and 4.4). In contrast, exotic richness showed generally positive relationships with both cover and biomass.

Disturbance level (treatment) was not a strong predictor of richness at the whole plot level, and it generally explained little deviance (less than 3%; Table 4.2). Treatment was a more important predictor of quadrat-level richness, and was selected third for both exotic and overall richness and fourth for native richness, though it again explained relatively little deviance (3-5%; Table 4.2).

Discussion

Our finding that the relationship between disturbance and richness was usually neither strong nor unimodal is consistent with recent reviews of disturbance-diversity relationships (e.g. Mackey and Currie 2001). We did not see a large difference in the observed richness-disturbance relationships when measured at different spatial scales; the relationship was generally weak and variable at both 625 m^2 and 1 m^2. However, we noted different patterns of diversity under different rainfall conditions and for native and exotic species, and this provides evidence that the variability in reported diversity-disturbance relationships is likely due in part to environmental factors and characteristics of the species. We also saw differences in the degree of response to disturbance across

our habitat-related productivity gradient such that the most productive habitat showed the widest range of responses to the experimental disturbance gradient as environmental conditions changed. This supports the idea that diversity-disturbance relationships are mediated by habitat productivity and depend strongly on the rate at which individuals are able to re-colonize or re-grow after disturbance (Huston 1979, White and Jentsch 2001).

There were consistent relationships between species richness and standing biomass or vegetation cover, and in almost all cases these were hump-shaped. The pattern persisted at the 625 m^2 scale (though the curvature tended to be less pronounced), indicating that it was not due solely to a tendency for higher biomass or cover quadrats to contain fewer but larger individuals (the "no interaction" model; Oksanen 1996).

Each 1m^2 quadrat sampled a reasonably large proportion of the species pools available in 625 m^2 (30% for alluvia and grasslands; 21% for woodlands), and this may account in part for the similarity in patterns across scales. Each 625 m^2 experimental plot contained between 16% and 21% of the total number of species available for each habitat in the Burrendong study area (approximately 60 km^2). A survey of 34 white box woodland remnants by Prober and Thiele (1995) tallied 309 species (179 native and 130 exotic) in white box remnants in the central west region of New South Wales; the woodland habitat at Burrendong contains over 60% of the species found in the regional species pool for White Box woodlands. These ratios are all reasonably high, and suggest that the largest variation in species richness may be at a very small scale in white box woodland remnants, a common pattern in grassland and savannah ecosystems (e.g. Lunt 1990, Klimeš 1995). This provides further evidence that the patterns observed in our study are not artefacts of using small sample plots.

Mechanistic explanations of the "hump-back" relationship between standing crop and richness are based on differences in competitive ability and growth form among species that may occupy a site (Milchunas *et al.* 1988, Oksanen 1990, White and Jentsch 2001). Many of the exotic species that have invaded box woodlands are grazing and disturbance tolerant weeds, while native species are grazing sensitive, drought tolerant perennial grasses and forbs. The native and exotic components of woodland flora could be expected to show different patterns of diversity in relation to disturbance, habitat productivity, and standing crop, and this has been observed previously in temperate Australia (McIntyre and Lavorel 1994). Though the general assumption is that perennial species (K-selected, or competitors) should dominate at high biomass or cover and annual weedy species (r-selected, or colonizers) should dominate at lower biomass or cover, we observed the opposite trend. We found that the richness of the annual exotic component of the flora tended to increase with increasing biomass or cover (while still showing a hump-shaped relationship), and the native perennial component tended to decrease.

In their recent simulation models, Mouquet *et al.* (2002) were able to produce a hump-shaped productivity-diversity relationship by assuming a strict tradeoff between competitive and colonization ability of species in their species pool (their CC model). However, this tradeoff does not necessarily exist because successful colonizing species (e.g. annual weeds) may compete for space by rapid vegetative growth for a short period, then continue to occupy that space after their death, particularly in low-disturbance environments (Bergelson 1990, K. Allcock personal observation). Consequently, a high-biomass environment does not necessarily favour K-selected species, and the existence of a hump-shaped relationship between biomass or cover and species richness is possible

even without a competition-colonization trade-off. The ability of colonizing species to grow quickly in favourable environments and to pre-empt space after death is likely a mechanism behind the richness-productivity relationships observed in our study.

Conclusions

We found the following results with respect to our three objectives:

1. Environmental variables (season and rainfall) appeared to be the most important determinants of species richness, followed by productivity related variables, and then disturbance. This pattern held true at both spatial scales.
2. The relationship of richness to both biomass and cover was strong and hump-shaped, while the richness-disturbance relationship was weak, variable, and influenced by environmental conditions. These patterns did not change with spatial scale.
3. Exotic species and native species showed different patterns of richness in relation to disturbance, productivity, and environmental conditions.

We observed little evidence for a hump-shaped relationship between richness and disturbance at either spatial scale, while both environmental variables and productivity variables (cover and biomass) were strongly related to species richness at both spatial scales. The effects of disturbance, although weak and variable, were slightly more obvious at the 1 m^2 sampling scale. The shape of the richness diversity relationship was strongly dependent on environmental and seasonal variation. Our results show that the shape of the relationship between diversity and disturbance depends strongly on

environmental conditions and the characteristics of the species involved. Altering these two factors can produce the entire range of observed diversity-disturbance relationships.

In contrast, richness showed consistent unimodal relationships to standing biomass and vegetation cover. We observed little difference in the richness patterns at 1 m^2 and 625 m^2 sampling scales, in contrast to other studies (Wieher 1999, Stohlgren *et al.* 2002). The curvature in the relationship of richness to biomass or cover tended to be stronger at the 1 m^2 scale, however, the shapes of the relationships were similar at both scales.

Climate, season, and species origin were important in determining richness-disturbance-productivity relationships. Productivity measures (cover and biomass) generally explained one tenth as much variability in species richness as did season. In addition, native box woodland species (predominantly perennial grasses) and exotic species (predominantly annual weeds) showed different patterns of species richness in relation to standing crop and total cover, with exotic species tending to increase in richness with increasing biomass or cover, and native species tending to decrease. The characteristics of the species involved are important in determining the shape of the productivity-diversity relationship. The ability of weedy annual species to grow rapidly and to pre-empt space after death is a possible mechanism for the hump-shaped relationships observed in this study.

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Table 4.1: Repeated measures ANOVAs (univariate mixed model, type III sums of squares) of total, native, and exotic species richness in spring (Sp) and summer (Su) from 1997 to 2001 in 625 m^2 experimental plots and 1 m^2 quadrats (nested in experimental plots) across four grazing treatments and three habitats. *p<0.01, ** p<0.001, *** p<0.0001.

Effect	d.f.		F (total)		F (native)		F (exotic)	
Plot	***Sp***	***Su***	***Sp***	***Su***	***Sp***	***Su***	***Sp***	***Su***
Habitat	2,36	2,36	**45.94*****	3.19	**91.03*****	**73.48*****	2.21	**45.47*****
Treatment	3,36	3,36	2.92	0.86	1.65	2.80	3.52	1.36
Hab*treat	6,36	6,36	1.50	0.53	0.67	2.38	1.25	1.14
Year	1,36	3,108	0.29	**18.18*****	2.42	**13.13*****	**7.96***	**18.52*****
Year*hab	2,36	6,108	1.34	**7.55*****	4.41	**4.58****	0.68	**7.68*****
Year*treat	3,36	9,108	1.69	2.06	0.35	0.50	2.63	**3.47****
Year*hab*treat	6,36	18,108	0.26	0.59	0.41	0.39	0.18	0.50
Quadrat	***Sp***	***Su***	***Sp***	***Su***	***Sp***	***Su***	***Sp***	***Su***
Habitat	2,36	2,36	**38.08*****	**14.28*****	**47.00*****	**16.62*****	**11.30****	**94.52*****
Treatment	3,36	3,36	**15.06*****	2.83	3.10	3.65	**20.09*****	**5.04***
Hab*treat	6,36	6,36	2.16	1.33	1.64	1.88	2.16	0.35
Year	1,900	3,1825	**96.93*****	**278.9*****	**67.87*****	**153.4*****	**96.93*****	**380.6*****
Year*hab	2,900	6,1825	**11.16*****	**15.56*****	**31.42*****	**21.87*****	**11.16*****	**20.50*****
Year*treat	3,900	9,1825	**12.06*****	**3.48*****	1.45	**4.10*****	**12.06*****	**4.40*****
Year*hab*treat	6,900	18,1825	**3.31****	**2.78****	**3.46***	**3.60*****	**3.31****	**3.36*****

Table 4.2: Variables selected by GLM models for total, native, and exotic species richness in whole plots ($625m^2$) and quadrats ($1\ m^2$, ten quadrats averaged per plot) (see Figs 3 and 4 for graphical representation of the relationships between richness and biomass or cover). Rank is the order in which the variables were selected in a forward stepwise procedure, Dev is the percent total deviance explained by each variable, and Coeff is the coefficient associated with each variable. Ranks and percent deviance are not listed for first order terms for biomass or cover when second order terms were selected; the values presented for second order terms represent both terms of the polynomial relationship. For categorical variables, (n-1) coefficients are presented. Coefficients are presented in the following order: for season, coefficient is for summer (spring=0); for habitat, coefficients are for woodland then grassland (alluvia=0); and for treatment coefficients are for control, stock exclusion, and kangaroo + stock exclusion (complete exclosure=0). Coefficients for interaction terms have been omitted for clarity.

Table 4.2.

	All species			Native species			Exotic species		
Whole plot	**Rank**	**Dev**	**Coeff (SE)**	**Rank**	**Dev**	**Coeff (SE)**	**Rank**	**Dev**	**Coeff (SE)**
Season	1	37.3	-0.11(0.02)	NS	-	-	1	57.7	-0.32(0.02)
Habitat	2	10.7	0.05(0.01) 0.06(0.01)	1	46.3	0.17(0.02) 0.13(0.02)	NS	-	-
Rainfall	4	0.8	0.005(0.001)	4	1.8	0.006(0.001)	NS	-	-
Months	5	1.6	0.002(0.001)	NS	-	-	NS	-	-
Biomass	-	-	-0.09(0.26)	-	-	0.12(0.54)	3	0.3	0.07(0.02)
Biomass^2	6	1.1	-0.58(0.2)	3	2.0	-1.6(0.45)	NS	-	-
Cover	-	-	-0.04(0.3)	-	-	-1.4(0.52)	-	-	1.0(0.52)
Cover^2	3	8.5	-1.2(0.2)	2	5.9	-1.4(0.34)	2	7.5	-1.6(0.41)
Treatment	NS	-	-	5	2.3	-0.05(0.02) 0.02(0.01) -0.02(0.01)	NS	-	-
Hab*Bio	NS	-	-	6	3.9	-	5	1.1	-
Hab*Cov	7	2.1	-	7	1.3	-	4	1.2	-
Tre*Month	NS	-	-	NS	-	-	6	1.9	-
Tre*Rain	NS	-	-	NS		-	NS	-	-
Quadrat									
Season	6	1.3	-0.11(0.04)	6	1.3	0.1(0.05)	1	65.9	-0.41(0.06)
Habitat	4	3.1	0.12(0.02) 0.02(0.02)	1	26.5	0.19(0.03) 0.07(0.03)	6	0.6	-0.002(0.03) -0.07(0.03)
Rainfall	1	55.5	0.014(0.002)	5	3.5	0.01(0.002)	4	2.7	0.02(0.003)
Months	NS	-	-	NS	-	-	NS	-	-
Biomass	-	-	-0.42(0.53)	3	6.7	-0.0002 (0.0001)	-	-	-0.43(0.63)
Biomass^2	2	10.1	-1.4(0.40)	NS	-	-	5	1.0	-1.4(0.51)
Cover	-	-	0.66(0.62)	-	-	-0.08(0.76)	-		2.5(0.97)
Cover^2	5	2.5	-1.8(0.41)	2	11.8	-2.0(0.50)	2	8.0	-4.0(0.62)
Treatment	3	3.6	-0.10(0.03) -0.04(0.02) -0.03(0.01)	4	5.0	-0.13(0.04) 0.03(0.02) 0.01(0.02)	3	5.2	-0.09(0.04) -0.1(0.02) -0.07(0.02)
Hab*Bio	NS	-	-	NS	-	-	NS	-	-
Hab*Cov	NS	-	-	NS	-	-	NS	-	-
Tre*Month	NS	-	-	NS	-	-	NS	-	-
Tre*Rain	NS	-	-	NS	-	-	NS	-	-

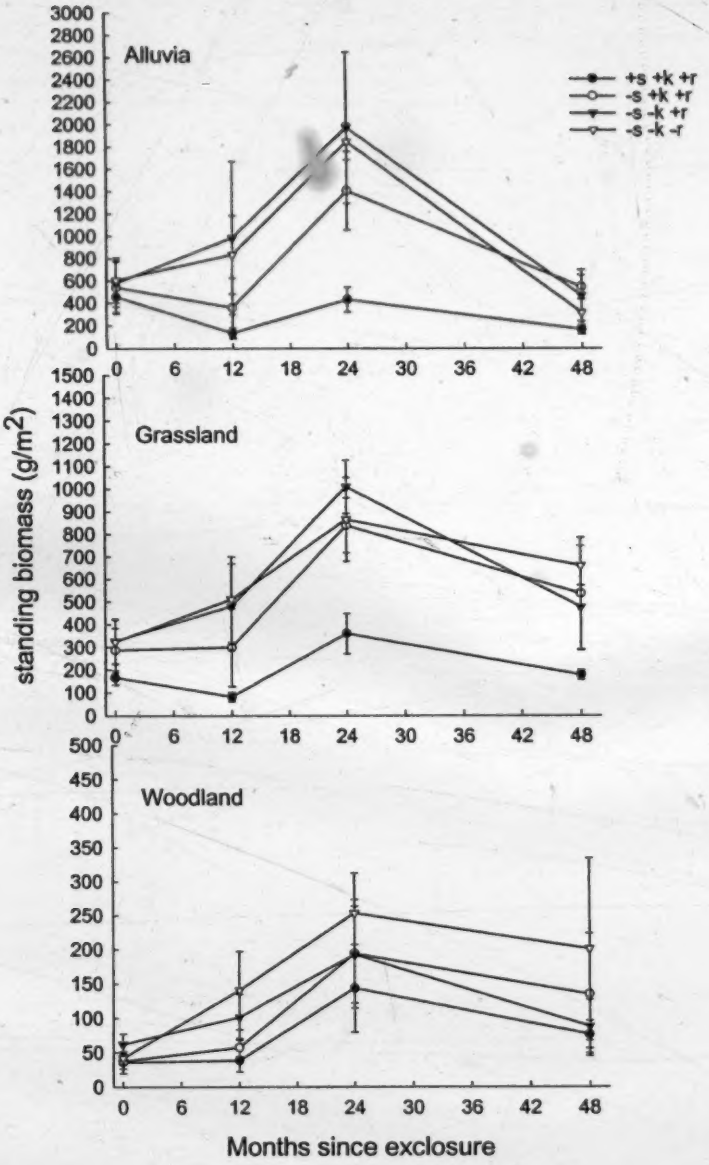

Figure 4.1: Standing biomass in summer (±S.E.) under four grazing disturbance treatments in three habitats, sampled 0, 12, 24, and 48-months after the treatments were initiated. The treatments were: unfenced, with grazing by stock, kangaroos, and rabbits (+s +k +r); stock fence, with grazing by kangaroos and rabbits (-s +k +r); kangaroo fence, with grazing by rabbits only (-s -k -r); and rabbit fence, with no grazing by vertebrate herbivores (-s -r -k). Exclosures were established in March 1997 (0 months) and sampled in March 1998 (12 months), March 1999 (24 months) and March 2001 (48 months).

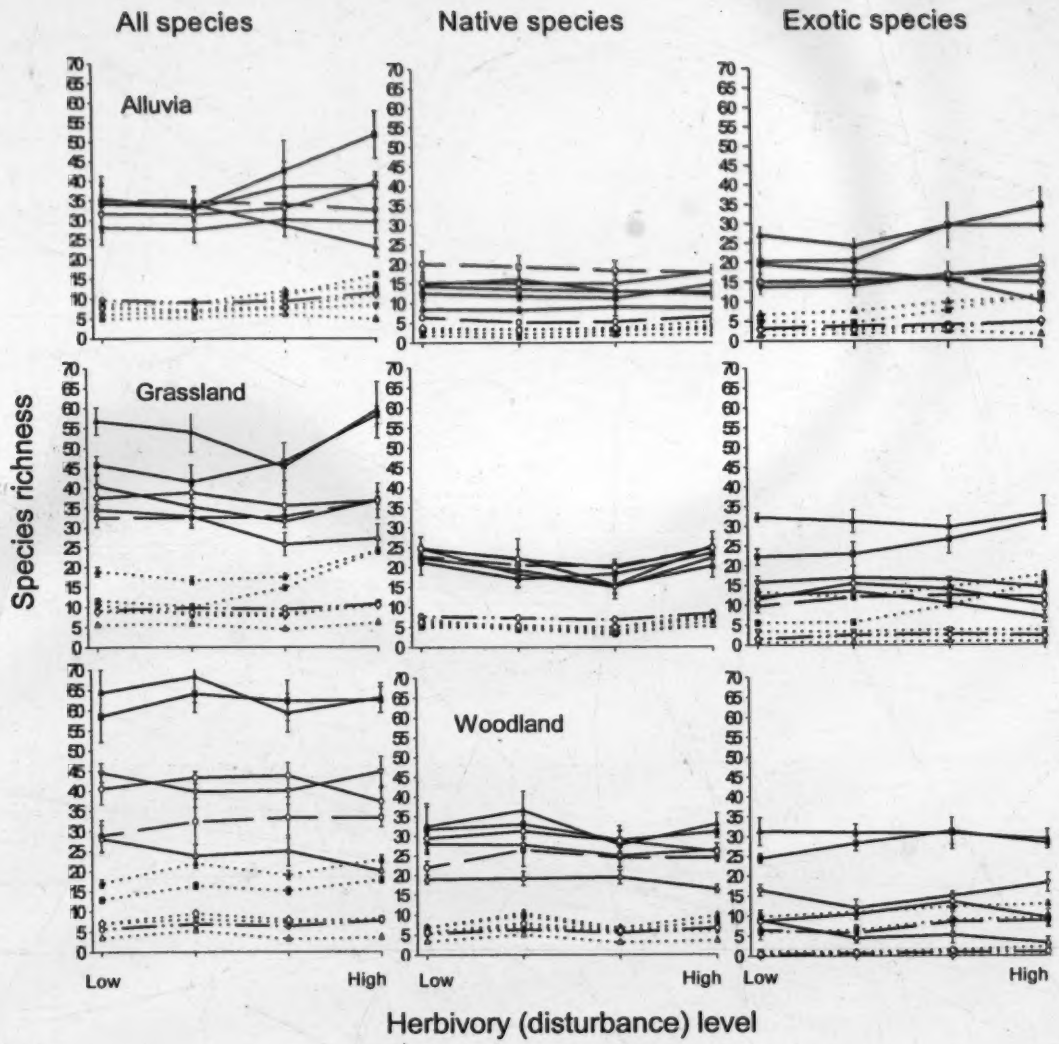

Figure 4.2: Total, native, and exotic species richness (±S.E.) in 625 m^2 experimental plots (solid lines) and 1 m^2 quadrats (dotted lines) in three habitats along a disturbance gradient created by grazing exclosures. Richness at the beginning of the experiment (March 1997) is represented by dashed (plot) or dotted-and-dashed (quadrat) lines. Samples were taken in March 1997 (open circles), March 1998 (open triangles), October 1998 (solid triangles), March 1999 (inverted open triangles), October 2000 (solid squares), and March 2001 (open diamonds). March 1998 sampling followed a period of drought, while October 1998 and March 1999 followed a period of unusually high rainfall.

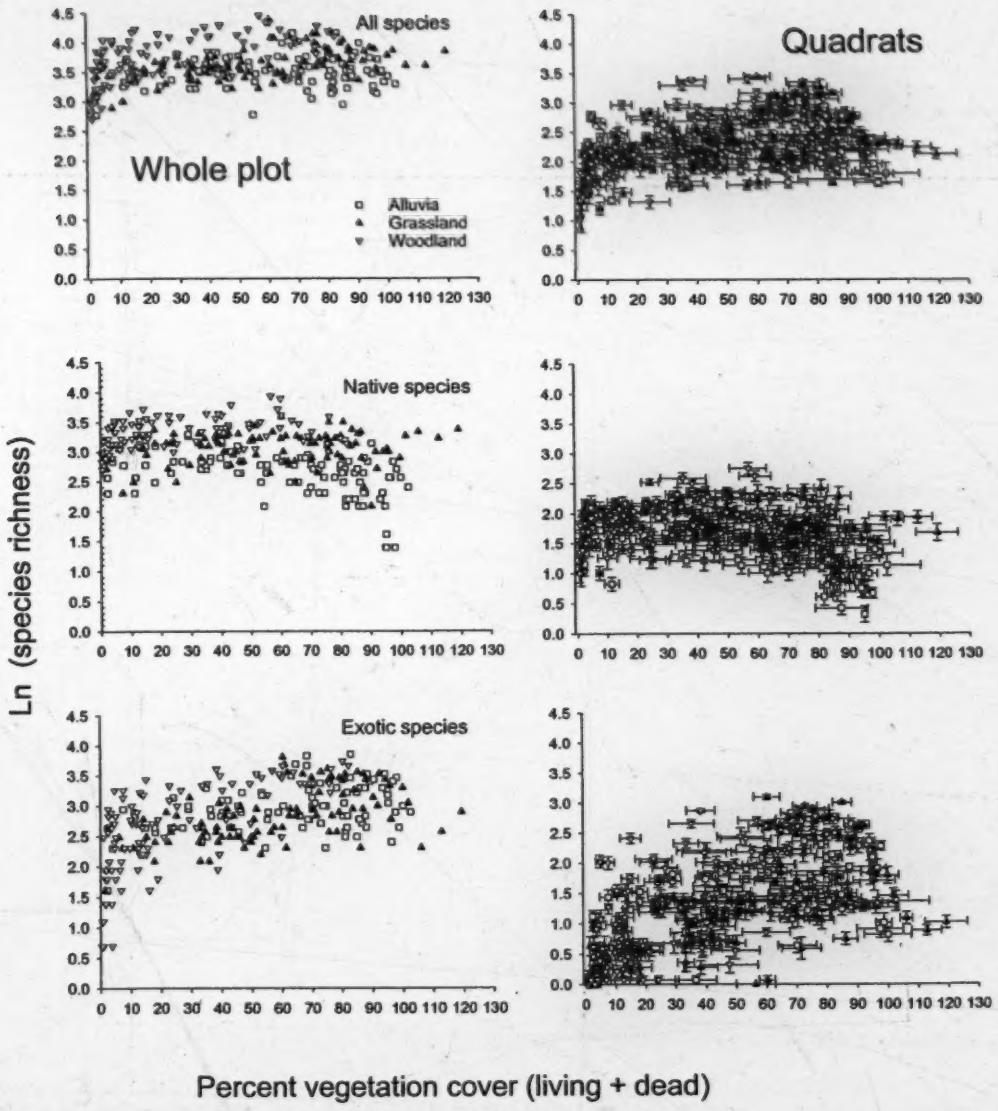

Figure 4.3: Total, native, and exotic species richness (log-transformed) versus vegetation cover (living plus dead material) for 625 m^2 experimental plots and 1 m^2 quadrats in three habitats. Vegetation cover estimates are mean cover in ten permanent quadrats (±S.E.) within each experimental plot. Quadrat richness estimates are mean richness in ten permanent quadrats (±S.E.) within each experimental plot. First and second order coefficients of the polynomial relationships between cover and richness are presented in Table 4.2.

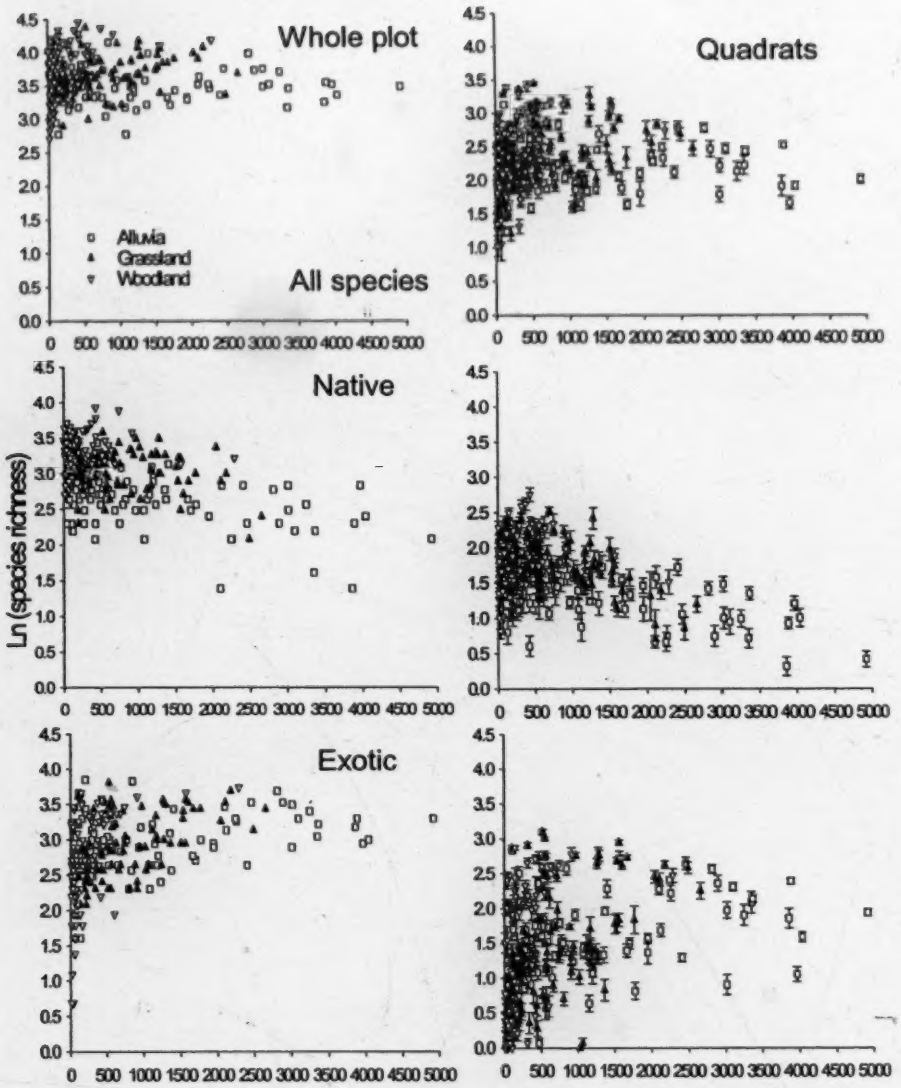

Figure 4.4: Total, native, and exotic species richness (log-transformed) versus standing crop for 625 m^2 experimental plots and 1 m^2 quadrats in three habitats. Quadrat richness estimates are mean richness in ten permanent quadrats (±S.E.) within each experimental plot. First and second order coefficients of the polynomial relationships between biomass and richness are presented in Table 4.2.

Chapter 5

Response of vegetation and soils to removal of grazers: a four-year experiment in Australian White Box woodlands[1]

Introduction

Herbivory has the potential to dramatically influence the structure and composition of plant communities (Huntley 1991, Ritchie and Olff 1999), and the effects of grazing may differ among communities with different productivity or evolutionary histories, or in the presence of different herbivores (Milchunas and Lauenroth 1993, Ritchie and Olff 1999). The effects of grazing are particularly important in structuring grassland and savannah ecosystems, even those without a long evolutionary history of herbivory, because many such ecosystems are currently utilized for domestic stock production (e.g. Noy-Meir *et al.* 1989, Pettit *et al.* 1995, Walker *et al.* 1997, Perevolotsky and Seligman 1998, Stampfli and Zeiter 1999, Stohlgren *et al.* 1999, Austerheim and Eriksson 2001).

Exclosure studies are frequently used to demonstrate the influence of herbivory on species composition or diversity, soils, and productivity in grazing systems (e.g. Milchunas *et al.* 1988, Noy-Meir *et al.* 1989, Grice and Barchia 1992, Rosenstock 1996, Hartnett *et al.* 1996, Brejda 1997, Stohlgren *et al.* 1999). Such studies measure the effect of herbivore removal rather than herbivory, and the reliability of the sampling methods used in some studies has been questioned (e.g. Stohlgren *et al.* 1999). However, these studies have proven particularly useful in demonstrating the extent to which herbivores affect vegetation (e.g. McNaughton *et al.* 1996, Hester *et al.* 2000). The exclosure approach is especially appropriate where there is concern over long-term grazing effects

[1] Manuscript currently being edited and formatted for submission to *Plant Ecology*.

and where reduction of herbivory may be used as a technique to conserve or restore ecosystems (e.g. Sluiter *et al.* 1997, Brejda 1997, Stohlgren *et al.* 1999, Yates *et al.* 2000).

In these cases, it is essential to determine whether exclusion of herbivores will have the desired effect on the vegetation because changes caused by intense or sustained grazing (especially at levels that would cause conservation concern) are not always reversible. Changes in soil characteristics (e.g. Brejda 1997, Yates and Hobbs 1997a), loss of species from the species pool (O'Connor 1991, Spooner *et al.* 2002), exotic weeds (Brown and Rice 2000, Yates *et al.* 2000), or lack of appropriate environmental conditions (Westoby *et al.* 1989) may prevent recovery and create boundaries between vegetation states.

Temperate woodlands in Australia provide an example of a system that has been drastically changed in recent years by an increase in herbivory (Yates and Hobbs 1997b). In southeastern Australia, white box (*Eucalyptus albens* Benth.) woodlands originally extended the length of New South Wales from Queensland to the Victorian border along the western side of the Great Dividing Range (Prober and Thiele 1993). These woodlands consisted primarily of well-spaced mature trees over an understory of native caespetose grasses (*Themeda australis* and *Poa sieberiana* dominant) and perennial forbs, with scattered shrubs (Prober and Thiele 1993). Grazing by domestic stock and feral rabbits, tree clearing, fire suppression, fertilization and invasion of exotic weeds dramatically changed the woodlands (Prober and Thiele 1993, Yates and Hobbs 1997b, Sivertsen and Clarke 2000).

Sustained stock grazing in particular caused dramatic shifts in species composition, first leading to dominance by cool season native grasses (*Austrostipa* and *Austrodanthonia* spp.), then to drought and grazing tolerant native species and exotic annual species (Moore 1970). Rabbit control and fencing to exclude domestic stock from remnants is the most widely applied restoration technique in white box woodland (e.g. Elix and Lambert 1997), with the hope that restoring grazing to its original intensity will allow remnant vegetation to recover (a common restoration approach in systems where introduced herbivores were the primary cause of degradation: Lamb 1993). However as noted previously, grazing-induced compositional changes are not always reversible and it is necessary to test whether boundaries or thresholds exist between current and desired vegetation states.

Our experiment was designed to assess the response of white box woodland vegetation and soils to grazing management, and to determine whether exclusion of herbivores from patches of remnant woodland would allow vegetation to recover, by becoming more similar to the presumed pre-European composition. We used a series of herbivore exclusion fences designed to exclude herbivores of successively smaller body size. These were placed in three habitats within the white box woodland mosaic (woodland remnants, cleared grassland or pasture, and alluvial valleys) and changes in the vegetation were monitored from 1997 to 2001 (four years), with the following objectives:

1. To assess changes in understorey composition in white box woodland habitats after following herbivore exclusion, and to determine whether variation in composition was attributable primarily to soil parameters, habitat, or fencing treatments.

2. To assess whether compositional changes consistent with vegetation recovery occurred following herbivore exclusion, and if so, which herbivores appeared to have the greatest influence on composition. Such changes would include reduction in exotic annual weeds and increase in native perennial grasses and forbs.

3. To determine whether soil condition and nutrient status changed following herbivore exclusion, and if so which herbivores appeared to have the greatest influence on soil parameters.

Methods

Study area

The study area is located at the confluence of the Cudgegong and Macquarie Rivers on the eastern foreshores of Burrendong Dam (32° 40' S, 149° 6' E), and is part of a large catchment administered by the Department of Land and Water Conservation of New South Wales. The climate is temperate with warm summers (mean maximum temperature 29° to 33°C) and cool winters (mean minimum temperature 2° to 3° C), and median annual rainfall of 666 mm (Bureau of Meteorology 1998). The Macquarie and Cudgegong Rivers were dammed in 1967 to create Lake Burrendong. The lower slopes of the foreshores were once dominated by white box (*Eucalyptus albens*) woodlands, but were largely cleared of trees in the 1800s to promote pasture growth. The lower slope grasslands are dissected by drainages running from the steep backing ridges to the lake, and along these drainage lines are patches of eeper alluvial soil. Farther from the lake shore, vegetation consists of white box woodland with grassy understory; white box, red box (*E. polyanthemos*), red stringybark (*E. macroryncha*), and mugga ironbark (*E.*

sideroxylon) forest with shrubby understory; rare stands of she-oak (*Allocasuarina verticillata*), and dense forests of cypress pine (*Callitris glaucophylla* and *C. endichleri*). Sheep and cattle are grazed under license, and there are large numbers of eastern gray kangaroos (*Macropus giganteus*; 15-38 sightings per spotlight kilometer, D. Hik and A. Newsome, unpublished data), wallaroos or euros (*M. robustus*) and swamp wallabies (*Wallabia bicolor*). Prior to July 1996, European rabbits (*Orictolagus cuniculus*) were extremely abundant. Rabbit haemorhagic disease (RHD) arrived at Burrendong Dam in the winter of 1996 and reduced the rabbit population substantially (by approximately 90% -Saunders *et al.* 1998); however, rabbits are still present at relatively high density (five sightings per spotlight kilometer, D. Hik and A. Newsome, unpublished data).

Experimental design

In February 1997, we established 25m by 25m exclosure fences to investigate the impact of grazing on understory vegetation in cleared (grassland), woodland, and alluvial areas, and to test for differences between the effects of different herbivores. The experiment was replicated in four blocks (each a creek watershed) spanning approximately 10 km. Within each block there were 12 experimental plots, evenly distributed in white box woodland (canopy intact), grassland (canopy cleared approximately 100 years ago), and alluvia. Some alluvial areas were too narrow to accommodate a square plot, so plots were made rectangular, 16.5m by 33m. Four treatments were applied in each habitat: control (T1: no fence), stock fence (T2: excluded sheep and cattle), kangaroo fence (T3: excluded sheep, cattle and all macropods), and rabbit fence (T4: excluded sheep, cattle, macropods, and rabbits), for a total of 48

experimental plots. Details of this design and photographs of the study area and treatment fences are provided in Chapter 1.

Sampling

1. Species cover and composition

Shortly after establishment of the experimental fences, 16 permanent 1m by 1m quadrats were marked in each plot. Quadrats were placed in a systematic grid, leaving a 3m buffer between the fence and the edge of the outermost quadrats. In rectangular plots, the grid was modified and 15 quadrats were marked and the outermost quadrats were 2.75 m from the long sides of the plots and 4m from the short sides. In each experimental plot, ten quadrats were randomly selected for permanent monitoring, and marked at lower left and upper right corners with 2cm by 2cm metal tags nailed flush with the ground. All permanent quadrats were measured four times in summer (March 1997, 1998, 1999, 2001) and twice in spring (October 1998, 2000).

For each quadrat we estimated the percent cover of each plant species present (ocular estimates of live foliar cover in $1m^2$) , as well as total vegetation cover, cover of standing dead plant material, and a variety of ground cover variables (litter, rock, bare soil, gravel, cryptobiotic crust, tree or shrub base, wood, and herbaceous plant basal area). Species or ground surface characters with a cover of less than 0.1% ($10cm^2$) were assigned a cover value of 0.05%. For subsequent statistical analyses, cover estimates for each species were averaged across quadrats to provide an estimate for each experimental plot. Nomenclature followed Hardin (1990-1993).

2. *Soils*

Indices of soil stability, infiltration capacity, and nutrient cycling were measured in March 1999 on each quadrat and were averaged for each experimental plot. These indices were determined following the Soil Surface Assessment component of the Landscape Function Analysis (LFA) technique (Tongway 1994). LFA was designed to provide landholders with a quick and informative assessment of soil stability, resource capture, and nutrient cycling on their property. The technique incorporates soil texture, cryptogam cover, evidence for erosion, litter cover and decomposition, erosion protection, microtopography, and perennial plant cover into three values indicating soil stability, infiltration capacity, and nutrient cycling capacity. These composite indices are generally highly correlated with standard chemical and physical soil measurements (Tongway and Hindley 2000a). The indices range in value from 0 to 1, with larger values indicating better soil or landscape function (resource retention). LFA soil surface characteristics were measured and LFA indices calculated for each permanent quadrat, then averaged to give one estimate for each 25m by 25m experimental plot. Details of the Landscape Function Analysis method are given in appendix 3 and are available at: www.cse.csiro.au/research/program2/LEP_LFA.htm.

Soil surface samples were collected from each experimental plot in April 2001 using a stratified random sampling design. Twenty random points were sampled per plot, and stratified into two bulked samples. Each sample was 4 cm in diameter and 2 cm deep. In grasslands and alluvia, samples were stratified based on the vegetation in a 25-cm radius surrounding the sample point into "annual" or "perennial" samples. To ensure that nutrient gradients around the bases of perennial tussocks did not introduce variability into

the measurements, all "perennial" samples were taken at a consistent distance of 2cm from surrounding perennial tussocks. In woodlands, samples were stratified based on whether they fell under the canopy of a white box tree or outside the canopy. "Canopy" samples were taken approximately midway between the bole and the dripline to minimize variation caused by a nutrient gradient surrounding the tree bole; "open" samples were taken outside the dripline of any trees.

Soil samples were air dried at ambient field temperatures (approximately 25 °C) for five days, then transported in sealed plastic bags to the CSIRO soil analysis lab in Canberra. Samples were sifted with a 3mm sieve, transferred to glass jars, dried for 3 days at 45°C and sealed. Dry samples were stored until November 2001 and then analysed for total carbon, total nitrogen and total sulphur (Leco CNS elemental analyser); available nitrogen (Gianella and Bremner 1986); available phosphorus (Colwell 1965); pH (1:5 soil in 0.01M $CaCl_2$) and electrical conductivity (1:5 soil in water) (Loveday 1974).

Data Analysis

Species composition

To assess the compositional response of vegetation to herbivore exclusion treatments and to partition variation into experimental, habitat-related and soils-related components, we used CANOCO v4.0 (ter Braak and Smilauer 1997) to conduct a series of canonical correspondence analyses (CCA) and partial ordinations (Legendre and Legendre 1998). Analyses were conducted on vegetation cover data from March 2001 (summer, 4 yr) and October 2000 (spring, 3.5 yr) after the experiment was initiated. Two sets of ordinations

were performed for spring data and two for summer data. Weighted averages of soil parameters were calculated for each experimental plot based on the number of samples bulked to provide each stratified sample (either annual/perennial or canopy/open). Species cover data were arcsine-square root transformed, soils data were ranged to between 0 and 1, and categorical data were converted to binary dummy variables. Ordinations were conducted to maximize inter-species distances and used bi-plot scaling (ter Braak and Similauer 1998, Legendre and Legendre 1998).

The variation decomposition procedure followed that used by Henderson and Kieth (2002), and required a series of eight ordinations to determine the compositional variation attributable to habitat and site, soil characteristics, and grazing treatments. The first ordinations and variation decompositions were based on cover of individual species within each experimental plot. Only species occurring in ten or more plots were included in this analysis (29 species in summer and 33 species in spring). Soil chemical parameters and LFA indices, and habitat, block, and grazing treatment were used variously as the environmental and covariate matrices in CCA and partial CCA analyses.

The second ordinations and variation decompositions were based on cover of pre-determined species groups. Species were grouped based on taxonomy (monocot forb, dicot forb, graminoid, grass, fern), species origin (native or exotic), growth form (low/creeping, tall/spreading, rosette-forming), life history (annual or perennial), and for grasses, the carbon pathway (C3 or C4). A total of 18 groups were defined (Table 5.1).

Vegetation changes

Changes in cover of species groups (calculated as (final cover)–(initial cover)) from March 1997 to March 2001 (summer) and from October 1998 to October 2000 (spring) were calculated, and then tested for the response of the most common species groups to our fencing treatments and to habitat using MANOVA. For summer samples, we used 12 of the 18 species groups; for spring samples we used 14 groups (Table 5.1). We assessed both the overall effects and the univariate responses of each species group to the factors.

Soils

We conducted principal components analysis (PCA) on soils data after ranging the data between 0 and 1 (Legendre and Legendre 1998). For this analysis we did not calculate weighted averages for each experimental plot, but used two stratified samples per plot (annual/perennial or canopy/open). The ordination was conducted to maximise inter-site distances.

To specifically test for soil differences between habitats and experimental treatments, we conducted a two-way MANOVA (SAS systems Inc. 1999) on a subset of soil parameters (total C, available N, available P, EC, and all LFA indices) with habitat and treatment as factors. The response variables were weighted average values of each soil parameter for each experimental plot (calculated as for the canonical ordinations). Total nitrogen and sulphur were strongly correlated with total carbon ($r > 0.8$), and were omitted from the MANOVA analysis. EC and pH were also strongly correlated, so only EC was included. We assessed both the overall effects and the univariate responses to treatment and habitat.

Results

Species composition: CCA and variation decomposition

CCA joint plots (using grazing treatment as canonical variables) indicated that the centroids for treatment effects were arrayed along the first CCA axis in order of decreasing level of exclosure (Figs 5.1 and 5.2). Complete exclosures (T4) and kangaroo + stock exclosures (T3) tended towards the negative end of CCA 1, while stock fences (T2) and unfenced plots (T1) tended towards the positive end of CCA 1. Sites, species and species groups were not well spaced along CCA 2 indicating that most of the variation when constrained by grazing treatment was explained in the first canonical axis. However, plots from different habitats showed some pattern along CCA 2 (Figs 5.1 and 5.2), with grasslands intermediate between alluvia and woodland.

In spring, four species (*Stipa scabra, Elymus scabrum, Danthonia racemosa,* and *Geranium solannderi*) were negatively associated with CCA 1 (Fig 5.1). The first three of these species are native perennial bunchgrasses with a C3 carbon pathway; the third is an erect native perennial forb. There were a number of species that were positively associated with CCA 1, including *Trifolium dubium, T. glomeratum, T. arvensis, Hypochaeris glabra, Arenaria serpifolia*, and *Panicum effusum.* The first five species are exotic annual forbs (three legumes) while the fourth is a disturbance tolerant native perennial grass with C4 carbon pathway (Fig 5.1). In summer, CCA 1 was again negatively associated with several native C3 grasses (*Dichelachne micrantha* and *Stipa scabra*) as well as two trailing native perennial forbs (*Glycine tabacina* and *Sida corrugata*), an exotic annual grass (*Bromus molliformis*) and an exotic weedy forb (*Chondrilla juncea*). CCA 1 was positively associated in summer with two native C4

grasses (*Chloris truncata* and *Paspalidium aviculare*), one prostrate native forb (*Chamaecyce drummondii*) and an exotic rosette forming noxious weed (*Echium plantagineum*) (Fig 5.1).

The canonical ordinations based on *a priori* species groups showed a similar pattern with treatments spaced in order of increasing disturbance along CCA 1 and some differentiation of habitats along CCA 2 (Fig 5.2). In spring, the NPFDT and NPGC3 groups (and, to a lesser extent, NPFM) were negatively associated with CCA 1, while EAL, EAFL, THIST, NAF (and, to a lesser extent, NPGM) groups were positively associated. In summer, NPFDT, NAF, and NPGC3 were negatively associated with CCA 1, while EPG, EAFL, NPGM, and EAFT were positively related (see Table 5.1 for acronym definitions and Appendix 1 for species included in each group).

Though the canonical ordinations produced interpretable patterns in species composition and species groups with respect to grazing treatments, the variation decompositions showed that treatment did not explain a large part of the variation in species composition or species group composition in the experimental plots (Table 5.2). In spring, the variation explained by treatment was between 6% and 8%; in summer it was below 5%. The combination of habitat and block explained considerably more variation (between 13% and 17%); habitat alone usually explained slightly less than half of this. Soil parameters explained between 15% and 18% of total variation, and the combination of habitat/block and soil parameters accounted for the largest proportion of variation in composition, ranging from 19.7% to over 25%. Taken together, the treatment, habitat/block, and soils-related variables explained a large proportion of total variation in species composition, generally around 60 to 65%.

Species composition: MANOVA of species groups

Table 5.3 shows the initial cover and change in cover for each species group in spring (a) and summer (b). In both spring and summer, habitat and grazing treatment significantly affected the change in cover of species groups from the beginning to the end of the experiment, and there was no significant interaction (Table 5.4). In spring, six of the 14 species groups tested showed significant univariate responses to habitat, treatment, or both. EAFR and EAG showed significant effects of both habitat and treatment; EAL, EPF and NPGC4 showed significant effects of habitat, and NPGC3 showed a significant treatment effect. In addition EAFR showed a significant habitat by treatment interaction. NAF, NPFDL, NPFDT, NPGM, EAFT, NPFM, and THIST showed no responses to treatment or habitat. In summer, five of the 12 species groups tested showed significant responses to treatment, habitat or both. EPF showed a significant effect of both habitat and treatment, while EAFL, EAFR, NAF, and NPGC4 showed significant habitat effects. In addition, EAFL showed a significant habitat by treatment interaction.

Least squares estimates and *a posteriori* comparisons of the univariate responses (based on data in Table 5.3) showed the following patterns with respect to treatment. In spring, cover of EAFR generally decreased from 1998 to 2000, but the decrease was much smaller in T3 and T4 (kangaroo fence and complete exclosures) than in T2 or T1 (stock fences or unfenced control plots). This trend was much more pronounced in grassland and alluvial habitats than in woodlands, accounting for the significant interaction term. NPGC3 increased in all treatments from 1998-2000, but the increase was larger in T3 and T4 than in T1 and T2. EAG showed a substantial decrease in cover in T3 and T4 compared to T1 and T2. NPGC4 showed an interesting pattern in cover

with respect to treatment, though the univariate response to treatment was marginally non-significant (p=0.06): T1 and T4 tended to show greater increases in cover of NPGC4 than did T2 or T3, and this was most evident in grasslands. In summer only EPF showed a significant treatment effect, with larger increases in cover in all fenced treatments (T2, T3, T4) compared to unfenced plots (T1). This was most evident in alluvial and grassland plots. Further investigation of the habitat by treatment interaction for EAFL indicated that in alluvial habitats T1 and T2 showed an increase in EAFL cover while all other treatments and habitats showed little or no change in cover.

Soils

Table 5.5 shows the mean values for each soil parameter in the stratified soil samples in each habitat and herbivore exclusion treatment. The PCA axes 1 and 2 explained a substantial proportion of variation among the samples (eigenvalues were 0.46 for PCA 1 and 0.20 for PCA2; combined variation explained 65%). Available N; total N, C, and S; and pH were strongly positively associated with axis 1 and less strongly with axis 2. Total N, C, and S were highly correlated ($r>0.8$ in all cases). EC and the three landscape function indices were negatively weighted on axis 1, and EC was strongly negatively correlated with pH. The three landscape function indices were the most influential variables on axis 2. Available P had little influence on either of the first two axes, and was most heavily weighted on axis 3, though it was positively related to axis 2. Differences in soil parameters among habitats were evident, with woodland and alluvial samples generally scoring higher on both axes than grassland samples (Figure 5.3), indicating generally higher values of all soil parameters except EC.

There were large differences between strata within each habitat, particularly between open and canopy samples in woodlands. Canopy and annual-dominated samples usually scored high on both axes indicating greater nutrient content, where samples from open areas or perennial-dominated locations tended to be lower on both axes. Annual patches in grassland or alluvial habitats were generally similar in soil properties to canopy patches in woodland, and perennial patches were similar to open woodland patches.

MANOVA of soil measurements (total C, available N, available P, EC, stability, infiltration, and cycling) showed an overall large habitat influence, with no treatment effect or treatment by habitat interaction (Table 5.6). Subsequent multiple comparisons showed that soils from all habitats differed from each other. Univariate comparisons showed habitat differences in total C (woodland carbon was higher than grasslands or alluvia), available N (woodland and alluvia had higher nitrogen than grassland), and LFA cycling index (the index was higher for woodlands and alluvia than for grasslands). Only the LFA cycling index showed a significant treatment effect, with all fenced treatments (T2-T4) having higher cycling indices than the unfenced treatment (T1). Available P showed a habitat by treatment interaction ($p=0.01$), but when habitats were analysed separately there was little effect of treatment in any habitat, and the significant interaction was likely due to high variation in P among alluvial sites.

Discussion

Species composition: sources of variation

The ordination analyses showed that the variation in species composition among sites may be attributed in part to the effects of our grazing treatments. Joint plots showed a

gradient in composition from T4 to T1 along CCA 1, with the largest differences apparently related to exclusion of stock and kangaroos (the centroids for T3 and T4 were generally close together and distant from the T1 and T2 centroids). In addition, there were several species and species groups that were associated either negatively (i.e. the direction of exclosure) or positively (the direction of grazing disturbance) with CCA1. Notably, native perennial tall forbs (e.g. *Geranium solanderi*) and native C3 grasses (e.g. *Dichelachne micrantha, Stipa scabra, Elymus scaber*) were negatively associated with CCA1, while exotic forbs (e.g. *Trifolium spp., Hypochaeris glabra, Echium plantagineum*) were positively associated. Two native C4 grasses (*Panicum effusum* and *Chloris truncata*) were also strongly positively associated with CCA1. Both of these grasses are generally considered grazing and disturbance tolerant, and may represent a stage in the degradation of native tall grassy understory under sustained grazing. According to Moore (1970), tall C4 grasses were replaced by C3 grasses then with exotic weeds and drought and grazing tolerant native species more common to semi-arid environments.

While there were interpretable patterns of composition in relation to fencing, fencing treatment explained very little of the variation in species composition or functional group composition in either spring or summer at the end of the experiment, especially compared with the effects of habitat and soil parameters. In fact, soil parameters alone or in combination with other variables accounted for approximately 40% of the total variation in both species and functional group ordinations. The variation shared by treatment and soil parameters was the largest explained variation component for species ordinations, while the variation shared by habitat and soil parameters was the largest explained

variation component for functional group ordinations. This implies that the responses of species and groups to either treatments or habitat characteristics are strongly mediated by soil parameters. It may also indicate that species were responding individually to grazing treatment while the characteristics used to create the functional groups were more related to habitat characteristics than to grazing tolerance.

Species composition: response to grazing treatments

The MANOVA results indicated that there were changes in the cover of species groups since the beginning of the experiment, and some of these changes indicated improvement in understory condition. For example, perennial C3 grasses have increased in cover by between five and 20% in T3 and T4 since the exclosure plots were established; this is encouraging from the standpoint of restoration, since native perennial grasses would certainly be a target for restoration. However, exclusion of stock alone appears to be insufficient to allow this increase (since there is no difference in C3 grass cover between T1 and T2), and control of macropod grazers may also be necessary.

There was some indication that C4 grasses were also affected by the grazing treatments but the patterns are less straightforward. C4 grass cover (at least in spring) was highest in either unfenced plots or complete exclosures and lower in the intermediate grazing treatments. This pattern likely indicated a shift in species composition within the C4 grass functional group, with low-growing disturbance- and drought-tolerant C4 species (e.g. *Panicum effusum, Chloris truncata*) dominating in unfenced plots, and taller casepetose C4 species (e.g. *Eragrostis molybdea, Digitaria brownii, Digitaria divaricatissima*) becoming more abundant in complete exclosures. Again, this shift is

consistent with improvement of understory condition with exclosure, but also indicates that stock exclusion alone is not sufficient for recovery.

While the native perennial grasses showed some signs of recovery with exclusion of both stock and kangaroos, most of the native species groups showed little or no change in cover with grazing exclusion. Native perennial forbs likely comprised much of the species diversity in pristine woodland and many species of this type are considered indicators of remnant health (e.g. *Microseris lanceolata, Leptorhynchos squamatus*: Prober and Thiele 1995); however, there was no significant effect of grazing treatment on cover of native forbs in either season, and variation in cover was high (Table 5.3a,b).

Most of the species groups that showed a response to the grazing treatments were of exotic origin. Exotic annual grasses and exotic annual low-growing forbs tended to decrease with exclusion of stock and kangaroos (especially in alluvial habitats); this is again encouraging for restoration efforts. However, in fenced plots, exotic annual grasses (notably *Bromus molliformis* and *Vulpia* spp.) showed substantial growth in early spring and by the time of sampling had died back to form a dense thatch that prevented growth of any other species (though *Bromus* and *Vulpia* seedlings were able to sprout). Because these annual species had often died before sampling, the dense swards were not included in the cover values. If thatch cover was included in the analysis, annual grass cover may have shown an increase with increasing protection. In addition, both exotic perennial forbs and exotic rosette-forming species increased in cover in fenced plots relative to controls in all habitats, and the increase in EPF cover was at least as substantial as the positive response seen for NPGC3 (about 25% increase in cover with fencing). Competition with exotic species can limit regeneration of native species (Yates and

Hobbs 1997b, Hamilton *et al.* 1999, Brown and Rice 2000). It appears that manipulation of grazing may be insufficient to allow recovery of native woodland understory in the presence of exotic weeds.

Soils

There was little effect of grazing exclusion on soil parameters. This finding contradicts that of Windsor (1998), who found an increase in soil carbon and a decrease in both nitrogen and phosphorus after only two years of herbivore exclosure. However it is consistent with other studies that have found little change in soil chemistry with exclusion of stock (e.g. Brejda 1997). Although LFA indices were assessed after only two years of treatment (time did not permit repetition of this sampling in 2001), there was some evidence that exclusion of stock improved the nutrient cycling capacity of soils. This was likely due to an increase in perennial grass cover and to accumulation of litter and perhaps reduction of soil compaction in the absence of hard-footed grazing animals. There was no change in the infiltration capacity or stability indices within the same time period. While it is possible that re-sampling LFA indices in 2001 would have shown changes in the infiltration and stability values, this is unlikely. Stability and infiltration were already reasonably high for all sites at Burrendong. In addition, nutrient cycling index generally shows the greatest difference between degraded and healthy rangeland sites (Tongway and Hindley 2000b). It is possible that with a gradual increase in native perennial grass cover and a reduction of annual legumes there might be a reduction in soil N and P; however, there is evidence that nutrient enrichment can both favour annual exotic species (e.g. Hobbs and Atkins 1988; Chapter 3) and cause a feedback in which

high-nutrient patches remain dominated by annual species and maintain their high-nutrient status (Eliason and Allen 1997). Overall there were large differences in soil parameters between annual-dominated and perennial dominated patches, between canopy and open patches in woodland, and between habitats in general. The nature of the soil-vegetation feedback (e.g. Wedin 1999) could help maintain the differences in vegetation and soils between habitats and patches even in the absence of grazing.

Barriers to restoration

Though there were modest indications of a shift towards a more native-dominated understory in fenced plots, the shifts were only evident when both stock and kangaroos were excluded, and no species that were not found in the above-ground vegetation at the beginning of the experiment had appeared after four years of exclosure. Species considered typical of less-disturbed white box remnants (e.g., *Themeda australis, Microseris lanceolata*) were absent, and it is very unlikely that the seed bank will be a source of propagules for regeneration of native understory (Board 2002). In addition, there was little effect of grazing treatment on total or native species richness, and native species richness declined with increasing vegetation cover and standing biomass (Chapter 4). Finally, there was an increase in cover of exotic perennial forbs and exotic rosette-forming annual forbs with exclosure, and little change in soil nutrient concentrations, which may be related to the degree of exotic species invasion (Hobbs and Atkins 1988, Cale and Hobbs 1991, Prober *et al.* in review). It appears that fencing may be an important step in restoring remnant white box woodland. However, excluding stock alone will not be sufficient and the loss of native species coupled with the presence of exotic

weeds and altered soil conditions indicate that boundaries exist between current and past vegetation states and further intervention will be required to overcome these (Prober *et al.* 2001, Chapter 6).

Because of the fragmented nature of remnant box woodland in Eastern Australia and the variability in remnant quality, woodland conservation and management will require a network of scattered reserves to represent the original ecosystem (Thiele and Prober 2000, Prober *et al.* 2001). As our study has shown, there is a strong "priority effect" in which the initial condition (vegetation composition, soils, and habitat characteristics) of a given remnant has an overwhelming influence on the potential vegetation composition and must dictate management options. In addition, the widely scattered nature of remnant woodlands means dispersal of species between remnants is unlikely. The Conservation Management Network (CMN) for grassy box woodlands allows for a range of management regimes across groups of sites with similar biological attributes or spatial location, and most of the remnants included in the CMN will be managed locally within the context of the network (Prober *et al.* 2001). The variability and isolation of remnants coupled with the strong priority effect means that an effective way to classify remnants and identify potential management challenges will be essential (Chapter 6).

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Table 5.1: Species groups included in ordinations (Ord) and MANOVA (M spr and M sum) analyses. The number of species in each group (Appendix 1) is also indicated.

Acronym	Species group	N	Ord	M spr	M sum
EAFL	Exotic annual low-growing forb	25	*	*	*
EAFR	Exotic annual rosette-forming forb	10	*	*	*
EAFT	Exotic annual tall or erect forb	42	*	*	*
EAG	Exotic annual grass or graminoid	28	*	*	*
EAL	Exotic annual legume	15	*	*	
EPF	Exotic perennial forb	15	*	*	*
EPG	Exotic perennial grass or graminoid	6	*	*	*
NAF	Native annual forb	35	*		
NAG	Native annual grass or graminoid	3	*		
NPFDL	Native perennial forb, low-growing dicot	23	*	*	*
NPFDT	Native perennial forb, tall dicot	24	*	*	*
NPFERN	Native perennial fern	2	*		
NPFM	Native perennial forb, monocot	11	*	*	
NPGM	Native perennial graminoid	11	*	*	*
NPGC4	Native perennial C4 grass	24	*	*	*
NPGC3	Native perennial C3 grass	17	*	*	*
NSHRUB	Native shrub or sub-shrub	11	*		
THIST	Thistle (all exotic)	7	*	*	*

Table 5.2: Percent of total variation in species composition attributable to herbivory exclusion treatment (Tr), habitat (Hab) and soil parameters (Soil) in experimental plots 3.5 (spring 2000) and 4 (summer 2001) years after exclusion of herbivores.

Component	Spring 2000 (species)	Spring 2000 (groups)	Summer 2001 (species)	Summer 2001 (groups)
Treatment	6.3	7.6	4.1	4.5
Habitat	16.7	13.7	14.8	14.8
Soils	18.9	14.7	15.7	17.0
Tr+Hab	0.8	1.9	2.6	1.9
Tr+Soil	20.0	4.9	19.6	1.8
Hab+Soil	4.5	25.2	2.8	31.7
Tr+Hab+Soil	-2.0	-2.6	-2.4	-1.4
Unexplained	34.7	34.6	42.8	29.7

Table 5.3 (a): Mean initial (Oct. 1998) and final (Oct. 2000) percent cover of species groups in spring in three habitats and under four herbivory exclusion treatments (I|F). T1=unfenced; T2=stock fence (sheep and cattle excluded); T3=kangaroo fence (sheep, cattle, and kangaroos excluded); and T4= complete exclosure (sheep, cattle, kangaroos and rabbits excluded). Cover values < 0.005% were reported as zero. Species groups in *italics* showed significant treatment effects in MANOVA. Differences in cover associated with treatment effects are highlighted in boldface.

	Alluvia				Grassland				Woodland			
Group	**T1**	**T2**	**T3**	**T4**	**T1**	**T2**	**T3**	**T4**	**T1**	**T2**	**T3**	**T4**
EAFR	75 | 21	53 | 8	**28 | 21**	**29 | 16**	27 | 6	**44 | 12**	**28 | 18**	15 | 5	8 | 1	15 | 5	8 | 0.3	4 | 0.4
EAG	**19 | 21**	26 | 15	44 | 17	55 | 30	**19 | 11**	34 | 13	44 | 12	**54 | 9**	5 | 1	13 | 3	8 | 1	13 | 2
EAL	10 | 12	14 | 3	8 | 1	3 | 0.7	31 | 12	18 | 6	9 | 0.4	8 | 0.3	13 | 1	20 | 3	21 | 2	20 | 3
EPF	0.3 | 8	1 | 25	0.8 | 18	1 | 12	0.1 | 9	0.3 | 16	0.2 | 17	0.2 | 15	0.4 | 2	0.4 | 2	0.4 | 6	2 | 2
NPGC4	1 | 5	0.7 | 2	0.1 | 0.3	0.1 | 2	**3 | 17**	1 | 6	2 | 6	**4 | 12**	0.4 | 0.3	1 | 1	1 | 3	1 | 3
NPGC3	0.3 | 7	0.4 | 6	**5 | 18**	**5 | 23**	0.6 | 3	0.6 | 8	**2 | 24**	**3 | 26**	2 | 4	1 | 6	**5 | 13**	**3 | 13**
NAF	2 | 0.4	2 | 0.4	1 | 0	1 | 0.1	8 | 0.1	1 | 0.1	1 | 0.1	1 | 0.02	2 | 0.1	4 | 0.1	2 | 0.2	2 | 0.1
NPFDL	1 | 4	1 | 1	2 | 2	1 | 1	1 | 19	1 | 4	1 | 2	3 | 2	5 | 12	4 | 13	8 | 17	8 | 14
NPFDT	0.3 | 1	0.7 | 3	2 | 6	2 | 4	0.4 | 0.4	0.2 | 0.8	0.6 | 1	0.6 | 3	3 | 3	3 | 2	3 | 4	5 | 9
NPFM	0 | 0	0.1 | 0	0 | 0	0 | 0	0.3 | 0.3	2 | 2	0.6 | 0.1	2 | 2	0.1 | 0.02	0.03 | 0.1	0.7 | 0.5	0.1 | 0.04
NPGM	0.03 | 0.8	0.2 | 3	0.02 | 1	0.8 | 0.2	0.1 | 1	0.2 | 0.8	0.02 | 1	0.04 | 0.3	0.3 | 0.6	0.1 | 1	0.1 | 4	0 | 0.03
EAFL	11 | 8	6 | 4	4 | 7	1 | 0.7	3 | 2	3 | 3	2 | 2	1.5 | 0.6	8 | 4	10 | 5	5 | 1	4 | 1
EAFT	1 | 3	0.4 | 1	6 | 0.3	0.5 | 0.3	1 | 1	0.3 | 0.1	0.3 | 0.2	0.5 | 0.7	3 | 0.2	4 | 0.5	1 | 0.5	1 | 1
THIST	6 | 1	1.5 | 1	1 | 0.1	0.6 | 0.5	5 | 6	3 | 7	3 | 2	3 | 3	4 | 0.7	8 | 3	3 | 0.3	9 | 0.4
EPG	0.1 | 0.1	0.3 | 1	0 | 0	0 | 0	0.7 | 0	0 | 0.3	0 | 0	0 | 0	0 | 0	0 | 0	0 | 0	0 | 0
NAG	0 | 0	0 | 0	0 | 0	0 | 0	0.04 | 0	0.03 | 0	0 | 0	0 | 0	0 | 0	0 | 0	0 | 0.04	0 | 0
NPFERN	0.04 | 0.2	0 | 0	0 | 0	0 | 0	0.2 | 0.3	0.1 | 0.1	0.3 | 0.03	0.7 | 0.3	0.3 | 0.2	0.05 | 0.2	0.8 | 0.9	0.4 | 0.3
NSHRUB	0 | 0	0 | 0	0 | 0	0.2 | 0.2	0 | 0.6	0 | 0	0 | 0	0 | 0	0.3 | 0.2	0.01 | 0.03	0 | 0	0 | 0.02

Table 5.3 (b): Mean initial (Mar. 1997) and final (Mar. 2001) percent cover of species groups in summer in three habitats and under four herbivory exclusion treatments (I|F). T1=unfenced; T2=stock fence (sheep and cattle excluded); T3=kangaroo fence (sheep, cattle, and kangaroos excluded); and T4=complete exclosure (sheep, cattle, kangaroos and rabbits excluded). Cover values < 0.005% were reported as zero. Species groups showing significant treatment effects in MANOVA are italicized. Differences in cover associated with fencing treatments are highlighted in boldface.

	Alluvia				Grassland				Woodland			
Group	**T1**	**T2**	**T3**	**T4**	**T1**	**T2**	**T3**	**T4**	**T1**	**T2**	**T3**	**T4**
EAFR	0.6 | 10	0.6 | 14	**4 | 29**	**0.3 | 17**	0.3 | 0.6	**1 | 5**	**0.2 | 4**	**0.1 | 1**	0.01 | 0.1	0.03 | 0.1	0 | 0.01	0 | 0
EAG	0.3 | 0.2	0 | 0.5	0.3 | 0.4	0 | 0.6	0.03|0.04	0.03 | 0.1	1 | 0.2	0.06|0.07	0 | 0	0 | 0.01	0 | 0	0 | 0.1
EAL	0 | 0.04	0 | 0.03	0 | 0	0 | 0	0 | 0	0 | 0	0 | 0	0 | 0	0 | 0	0 | 0	0 | 0	0 | 0
EPF	7 | 7	**0.8 | 21**	**0.2 | 21**	**0.2 | 21**	2 | 5	**1 | 20**	**2 | 21**	**1 | 20**	0.5 | 2	0.2 | 2	2 | 8	0.8 | 1
NPGC4	39 | 19	40 | 12	32 | 2	36 | 7	35 | 30	34 | 26	24 | 31	28 | 42	1.5 | 1	4 | 3	**4 | 10**	**3 | 6**
NPGC3	2 | 6	0.2 | 5	2 | 10	3 | 18	1 | 2	1 | 9	1 | 11	0.1 | 7	3 | 6	3 | 6	**3 | 11**	**1.5 | 9**
NAF	1 | 2	0.5 | 3	0.3 | 7	0.4 | 6	0.1 | 0.1	0.1 | 0.01	0.2 | 1	0.05 | 1	0.04|0.03	0.03|0.02	0.01|0.02	0.02|0.2
NPFDL	3 | 3	2 | 0.7	0.5 | 2	2 | 3	9 | 6	8 | 9	3 | 3	1.5 | 6	2 | 6	2 | 5	2 | 9	1 | 7
NPFDT	2.5 | 0.4	3 | 2	0.3 | 4	2 | 6	2.5 | 0.5	2 | 1.5	1.5 | 0.3	9 | 2	0.8 | 0.6	0.2 | 1	0.3 | 1	1 | 2
NPFM	0 | 0	0 | 0	0 | 0	0 | 0	0.04|0.06	2 | 5	0 | 0	0.02 | 0.1	0 | 0	0 | 0.07	0 | 0.1	0 | 0
NPGM	0.1 | 0.2	0.2 | 4	0.2 | 2	0 | 0.5	0.04 | 0.6	0 | 0.7	0.07|0.06	0 | 0.2	0.4 | 0.9	0.03 | 1.5	0.2 | 0.6	0 | 0.09
EAFL	2 | 4	0.6 | 6	0.8 | 0.8	0.2 | 0.1	0.2 | 0.1	0.4 | 0.01	0.1 | 0.1	0.01 | 0.1	0.02|0.04	0.05 | 0.1	0 | 0.04	0.01|0.03
EAFT	5 | 2	3.5 | 2	1.5 | 2.5	3 | 1	1.4 | 0.01	0.3 | 0	0.7 | 0.1	0.7 | 0	0.03|0.02	0.02|0.08	0.01|0.01	0.06 | 0
THIST	1 | 0.02	0.2 | 0.03	0.2 | 0	0.3 | 0.03	0.3 | 0	0 | 0.06	0.01 | 0.1	0.08|0.03	0.06|0.02	0.04|0.03	0.01 | 0	0 | 0.01
EPG	0 | 0.1	0.6 | 3	0 | 0.4	0.08|0.08	0 | 0.01	0 | 0.04	0 | 0	0 | 0	0 | 0.01	0 | 0	0 | 0	0 | 0
NAG	0 | 0	0 | 0	0 | 0	0 | 0	0 | 0	0.1 | 0	0 | 0	0 | 0	0 | 0	0 | 0	0 | 0	0 | 0
NPFERN	0.06 | 0.1	0 | 0.01	0 | 0	0 | 0	0.07 | 0.1	0.03|0.03	0.05|0.07	0.05 | 0.2	0.2 | 0.2	0.02 | 0.2	0.1 | 0.1	0.08 | 0.3
NSHRUB	0 | 0	0 | 0	0 | 0	0 | 0.6	0.1 | 0.3	0 | 0	0 | 0	0 | 0	0.2 | 0.1	0.03 | 0.1	0.06 | 0	0.1 | 0.05

Table 5.4: MANOVA of change in cover of *a priori* species groups from 1997-2001 (summer) and 1998-2000 (spring) with three habitats (alluvia, grassland and woodland) and four herbivore exclusion treatments (T1-T4) as factors.

Factor	Wilkes' lambda	F	DF (num,den)	p
Spring				
Habitat	0.086	3.96	28,46	**<0.0001**
Treatment	0.070	2.38	42,69	**0.0007**
Habitat*Treatment	0.045	1.19	84,134.6	0.18
Summer				
Habitat	0.070	5.80	24,50	**<0.0001**
Treatment	0.13	2.03	36,74.5	**0.005**
Habitat*Treatment	0.11	0.97	72,141.8	0.56

Table 5.5: Mean values of soil parameters in stratified soil samples from experimental plots. Variables sampled were total carbon (C), total sulphur (S) total nitrogen (N), available phosphorus (AP), available nitrogen (AN) electrical conductivity (EC), pH, stability (STA), infiltration (INF) and nutrient cycling (CYC). Units for C, S, and N are percent, units for AP and AN are ppm, and STA, INF, and CYC are dimensionless indices. Herbivore exclusion treatments are described in the text.

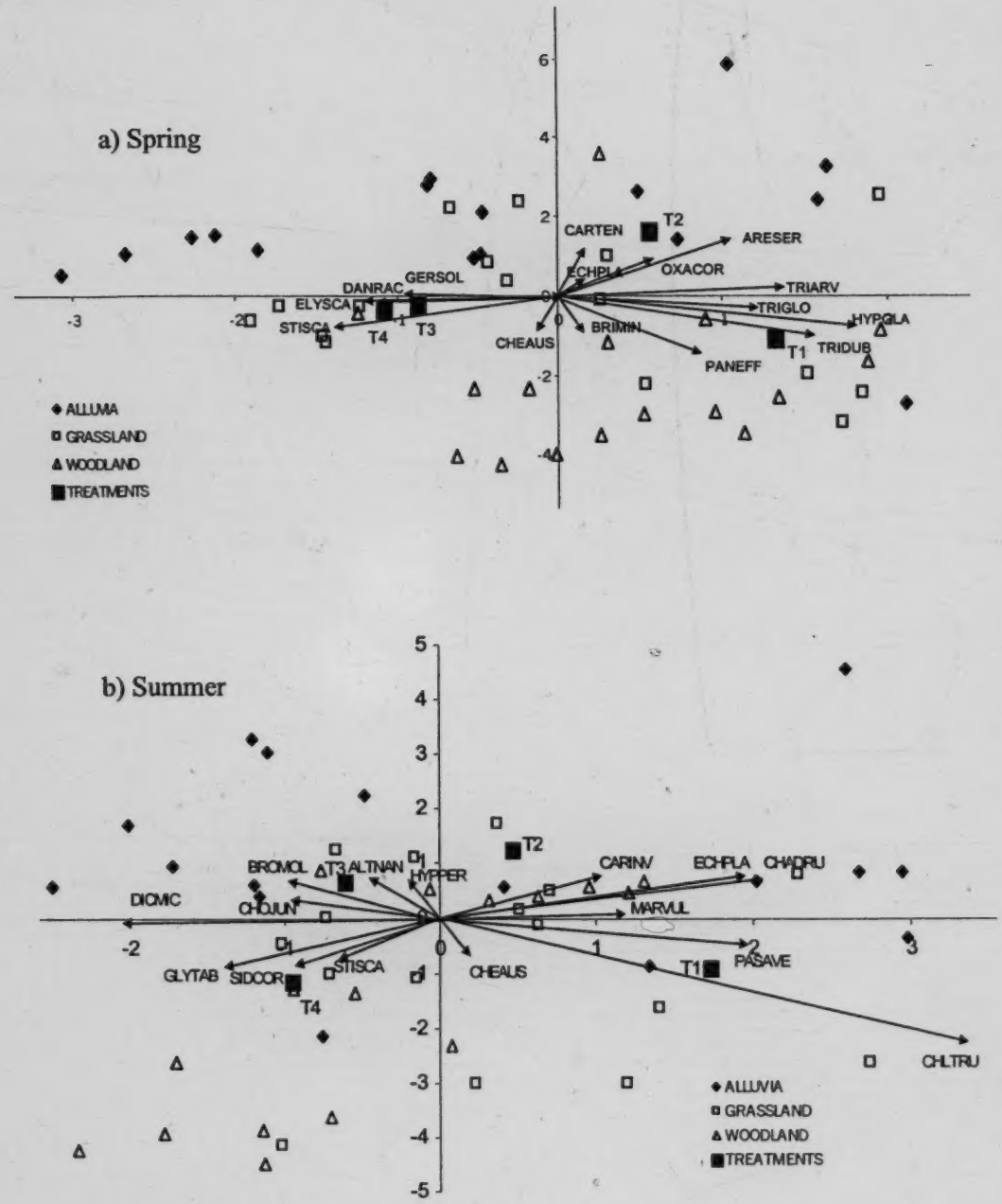
	C	S	N	AP	AN	EC	pH	STA	INF	CYC
Alluvia annual										
T1	6.6	0.054	0.65	27.3	81.8	71.5	6.36	0.66	0.52	0.38
T2	6.0	0.045	0.58	75.2	58.4	56.6	6.53	0.69	0.55	0.44
T3	7.6	0.058	0.71	33.6	86.9	70.3	6.33	0.67	0.55	0.46
T4	6.9	0.048	0.65	28.8	69.8	90.5	6.03	0.71	0.56	0.46
Alluvia perennial										
T1	6.0	0.048	0.57	26.4	66.7	85.3	6.18	0.66	0.52	0.38
T2	5.9	0.049	0.56	58.9	74.0	107.2	6.51	0.69	0.55	0.44
T3	6.9	0.054	0.65	15.3	74.2	123.6	6.38	0.67	0.55	0.46
T4	5.7	0.040	0.53	51.8	52.0	115.0	6.17	0.71	0.56	0.46
Grassland annual										
T1	5.8	0.045	0.55	31.6	47.9	60.1	5.8	0.65	0.51	0.33
T2	5.5	0.043	0.52	30.4	66.8	65.9	6.29	0.69	0.53	0.40
T3	6.1	0.047	0.59	26.7	51.9	45.8	6.31	0.68	0.54	0.41
T4	5.3	0.040	0.50	35.9	55.6	78.0	5.66	0.71	0.55	0.41
Grassland perennial										
T1	5.7	0.044	0.53	17.3	50.9	117.6	5.73	0.65	0.51	0.33
T2	4.9	0.037	0.48	36.9	47.9	82.8	6.25	0.69	0.53	0.40
T3	5.2	0.041	0.51	44.5	50.5	94.0	5.79	0.68	0.54	0.41
T4	4.5	0.039	0.43	37.0	45.8	94.7	5.63	0.71	0.55	0.41
Woodland canopy										
T1	10.1	0.047	0.71	41.0	48.5	60.8	6.68	0.67	0.54	0.39
T2	11.6	0.053	0.77	33.3	65.7	72.5	6.81	0.70	0.55	0.44
T3	10.4	0.049	0.69	48.0	52.8	53.0	6.84	0.71	0.54	0.42
T4	10.2	0.053	0.70	50.3	62.5	63.1	6.68	0.71	0.55	0.44
Woodland open										
T1	6.5	0.041	0.46	54.7	44.2	89.8	5.89	0.67	0.54	0.39
T2	5.9	0.030	0.45	23.1	41.5	104.9	6.05	0.70	0.55	0.44
T3	6.0	0.034	0.44	28.2	45.7	101.7	6.02	0.71	0.54	0.42
T4	5.9	0.031	0.44	24.6	47.4	97.5	5.73	0.71	0.55	0.44

Table 5.6: MANOVA of soil measurements (total C, available N, available P, EC, stability, infiltration, and cycling) with habitat (alluvia, grassland or woodland) and herbivore exclusion treatment (T1-T4) as factors.

Factor	Wilkes' lambda	F	DF (num,den)	p
Habitat	0.083	10.57	14,60	**<0.0001**
Treatment	0.458	1.29	21,86.7	0.2
Habitat*Treatment	0.30	1.02	42,144.2	0.45

Figure 5.1: CCA biplots (axes 1 vs 2) of species composition in Spring 2000 (a) and Summer 2001 (b) for 48 experimental plots in three habitats. Species scores have been multiplied by 3 to increase legibility. Eigenvalues for the first and second CCA axes are a) 0.00.082 and 0.00.022 for spring and b) 0.081 and 0.0.30 for summer. Only the species with the highest scores on axes 1 or 2 are shown. Grazing treatments (T1=unfenced control, T2=stock fence, T3=kangaroo+stock fence, T4=complete exclosure) were used as the canonical variables, with no covariates. Species abbreviations are: ALTNAN *Alternanthera nana*, ARESER *Arenaria serpyfolia,* BRIMIN *Briza minor,* BROMOL *Bromus molliformis,* CARINV *Carex inverse,* CARTEN *Carduus tenuiflorus*, CHADRU *Chamaecyce drummondii,* CHEAUS *Cheilanthes austrotenuifolia,* CHLTRU *Chloris truncata,* CHOJUN *Chondrilla juncea,* , DANRAC *Danthonia racemosa,* DICMIC *Dichelachne micrantha*, ECHPLA *Echium plantagineum,* ELYSCA *Elymus scaber,* GERSOL *Geranium solanderi,* GLYTAB *Glycine tabacina,* HYPGLA *Hypochaeris glabra*, HYPPER *Hypericum perforatum,* MARVUL *Marrubium vulgare,* OXACOR *Oxalis corniculata,* PANEFF *Panicum effusum,* PASAVE *Paspalidium aversum,* SIDCOR *Sida corrugata*, STISCA *Stipa scabra,* TRIARV *Trifolium arvensis,* TRIDUB *Trifolium dubium,* and TRIGLO *Trifolium glomeratum.*

Figure 5.1:


a) Spring
CARTEN
T2
ARESER
ECHPLA
OXACOR
DANRAC
GERSOL
TRIARV
ELYSCA
TRIGLO
HYPGLA
STISCA
T4
T3
CHEAUS
BRIMIN
T1
TRIDUB
PANEFF
ALLUVIA
GRASSLAND
WOODLAND
TREATMENTS
b) Summer
T2
BROMCL
T3
ALTNAN
HYPPER
CARINV
ECHPLA
CHADRU
DIOMIC
CHOJUN
MARVUL
GLYTAB
SIDCOR
STISCA
CHEAUS
T1
PASAVE
T4
CHLTRU
ALLUVIA
GRASSLAND
WOODLAND
TREATMENTS

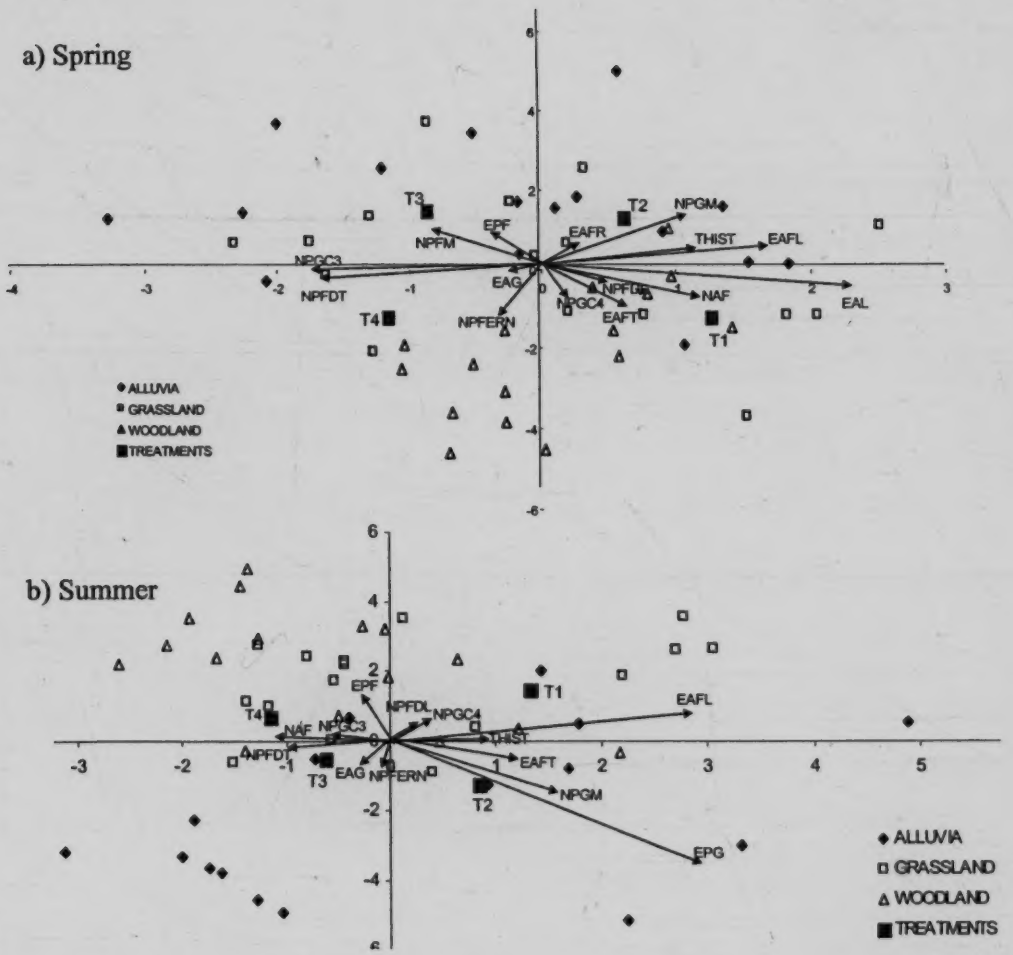


Figure 5.2: CCA biplots (axes 1 and 2) of *a priori* species group composition in Spring 2000 (a) and Summer 2001 (b) for 48 experimental plots in three habitats. Species group scores have been multiplied by 3 to increase legibility. Eigenvalues for the first and second CCA axes are a) 0.055 and 0.018 for spring and b) 0.024 and 0.015 for summer. Grazing treatments (T1=unfenced control, T2=stock fence, T3=kangaroo+stock fence, T4=complete exclosure) were used as the canonical variables, with no covariates. Species groups and acronyms are listed in Table 5.1.

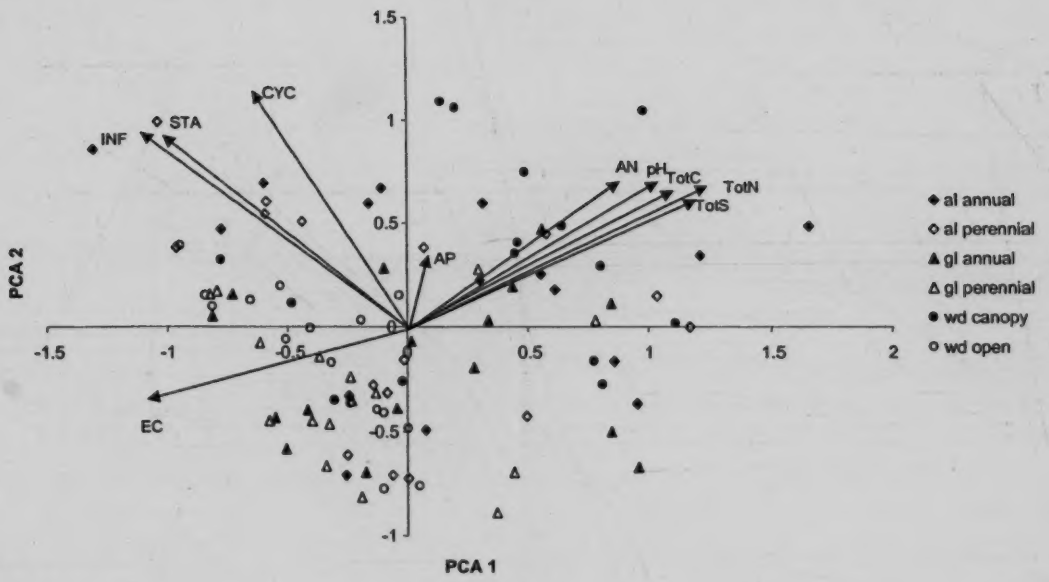


Figure 5.3: PCA biplot (axes 1 and 2) for soil properties, scaled to maximize differences between samples. Samples were stratified into canopy VS open for woodland (wd) habitat and annual VS perennial for grassland (gl) and alluvial (al) habitats. Soil parameters included in the analysis were total carbon (totC), total sulphur (totS), total nitrogen (totN), available nitrogen (AN), available phosphorus (AP), pH, electrical conductivity (EC), and indices of soil infiltration capacity (INF), stability (STA) and nutrient cycling capacity (CYC).

Chapter 6

Identifying asymmetric boundaries (thresholds) in state and transition models: challenges for restoration of white box woodlands[1]

Introduction

Vegetation responses to grazing disturbance have long been considered analogous to secondary succession (*sensu* Clements 1916, Smith 1989, Vayssieres and Plant 1998). The standard model for assessing condition of rangeland ecosystems, the "range condition" (RC) model (Dykerstuis 1949) assumes that rangeland vegetation undergoes a series of predictable and reversible compositional changes with changes in stocking pressure. However grazing systems do not always follow predictable paths of vegetation change with disturbance, and degraded rangelands may not always recover to a desired state with cessation of grazing (e.g. Laycock 1991, Hodgekinson and Cook 1995, Brejda 1997).

Herbivore activity can result in more than one stable vegetation state (Noy-Meier 1975, Dublin *et al.* 1990, Hik *et al.* 1992, Augustine *et al.* 1998). More sophisticated models of vegetation dynamics (carousel, multiple state, etc; Crawley 1986) have replaced the linear deterministic succession model in ecology, and in the past ten years the state and transition model (Westoby *et al.* 1989a,b) of rangeland dynamics has come to replace the range condition model (e.g. Vayssieres and Plant 1998).

The state and transition (S&T) model describes vegetation dynamics in terms of a set

[1] This manuscript will be edited and formatted for submission to *Ecosystems*.

of discrete 'states' that can occur on a particular site, and 'transitions' between these states that can be triggered by natural events (fire, weather) or management actions (change in stocking rate, fertilization) (Westoby *et al.* 1989a). Although the S&T model is based on discrete states with boundaries and transitions between them, a degree of variation is possible within each of the states. Thus the S&T model can incorporate classic RC dynamics within each vegetation state and still allow for state shifts and boundaries between states when transition conditions occur.

In the "ball and cup" analogy of resilience and multiple stable state systems (Holling 1973, George *et al.* 1992) RC dynamics would occur when perturbations move the 'ball' around within the basin of the cup; S&T dynamics would occur when the perturbations are large enough to shift the ball from one cup to another. As noted by Vayssieres and Plant (1998), the S&T model is not a new ecological theory but an efficient means of organizing knowledge about an ecosystem. This approach has several advantages. It is versatile, allowing for adaptive management, and in fact, this was the original intention of the S&T model (Westoby *et al.* 1989b). It is a useful way to organize knowledge of a system and can be refined as information improves. It is also possible to incorporate both qualitative and quantitative information into the framework. Finally, it allows for the identification of asymmetric boundaries and thresholds between vegetation states.

While the S&T approach was developed for and has been primarily applied in rangeland management, it is equally useful in a conservation context, particularly when habitats are fragmented or partially degraded and in need of restoration (e.g. Yates and Hobbs 1997a, Thiele and Prober 2000, Prober *et al.* 2001). An understanding of

threatening processes or barriers to restoration is essential for appropriate management of remnant habitats (Yates and Hobbs 1997b, 2000; Sivertsen and Clark 2000), and the S&T approach can be used to identify boundaries and compile what is known about ecosystems. As noted above, this approach may be especially useful in adaptive management, since it is possible to refine the models as more information is obtained. In fragmented ecosystems where limited dispersal, edge effects, local extinctions or disruption of natural disturbance regimes may have created boundaries between vegetation states, the S&T framework would be very advantageous.

One of the main features of S&T modelling is the ability to identify thresholds or asymmetric boundaries between ecosystem states. An asymmetric boundary is a transition between vegetation states that cannot be reversed by simply removing or reversing the disturbance that caused the initial shift. For example, a perennial grass population may collapse under sustained grazing and not recover when grazing pressure is reduced (e.g. Noy-Meier 1975, Hodgekinson and Cook 1995). Westoby *et al.* (1989a) suggested five mechanisms that could lead to asymmetric boundaries in grazing systems: (i) demographic inertia (rare or sporadic recruitment events), (ii) grazing catastrophe (population collapse), (iii) competition priority or space pre-emption (e.g. ability of adult plants to exclude seedlings of other species), (iv) positive feedback loops (e.g. fire promotion by fire-tolerant species), and (v) soil changes (e.g. plant-soil feedbacks). In addition, factors related to the species pool such as local extinction, introduction or invasion of new species, and dispersal limitation could be effective boundaries, especially in fragmented ecosystems.

Most S&T models are based on two methods of determining states and transitions. The first is a qualitative assessment of ecosystem changes, usually based on consultation with experts and historical descriptions of vegetation change (e.g. Yates and Hobbs 1997a, Allcock *et al.* 1999). The second is based on classification or ordination using a large number of sample points within identified vegetation types, and may include an investigation of spatial patterning where the history of disturbance is known (e.g. Bork *et al.* 1997, Plant *et al.* 1999). A combination of empirical and qualitative information may allow S&T models to be tested explicitly (Plant *et al.* 1999). Experimental evidence for asymmetric boundaries can be difficult to obtain because the system must be near a boundary and an experimental perturbation push the system across this boundary. In addition, the spatial and temporal scale must be large enough to demonstrate that the shift is "permanent" (Petraitis and Latham 1999). However, once the S&T framework has been developed based on expert opinion, classification, or historical records, this framework can be used to identify likely boundaries and to direct experimentation (Yates and Hobbs 1997a).

In this study, literature review and historical data were used to develop an S&T model for grassy white box (*Eucalyptus albens* Benth.) woodlands in the Central West Slopes region of New South Wales. A combination of field and laboratory experiments and vegetation/soil surveys were conducted to test the asymmetry of the identified boundaries. White box woodlands once stretched the length of New South Wales on the western slopes of the Great Dividing Range. They are now among Australia's most endangered ecosystems, with 0.01% of their original extent remaining in relatively good condition (Prober and Thiele 1993). They have been highly modified by grazing,

clearing, fertilization, invasion of exotic species, and agricultural activity, and currently exist as scattered remnants of varying quality, size, and landuse. The plan for conserving remnant white box woodlands relies on protecting high quality remnants from degradation and restoring poorer quality remnants to create a network of protected areas (Thiele and Prober 2000, Prober *et al.* 2001). Remnants are widely scattered, isolated, and variable in composition, and a variety of management regimes will need to be implemented (Chapter 5, Prober *et al.* 2001). Success will require the understanding of vegetation boundaries and threatening processes provided using the S&T framework (e.g. Prober *et al.* in review).

Development of an S&T model for white box woodland

We developed an S&T model for grassy white box woodland based on literature review, historic records, observations and expert description of remnant woodland patches, and the management history and vegetation of the eastern foreshores of Burrendong Dam NSW, the study site used for our subsequent field experiments. Figure 6.1 describes the model along with a catalogue describing proposed states and transitions. The literature sources used to define the S&T variables are listed in Table 6.1.

The original grassy white wox woodland community [S1] consisted of *E. albens* with an understory of perennial warm season grasses with scattered native forbs and occasional shrubs; *T. australis* and *Poa siberiana* were probably the dominant species (Moore 1970; Prober and Thiele 1993, Prober *et al.* 2001). Fire, light grazing by marsupials, and intermittent drought likely maintained this state. The introduction of stock in the early 1800's forced the original woodlands towards an understory dominated

by cool season perennials such as *Austrodanthonia* and *Austrostipa* [S2]. Clearing to improve pasture and subsequent grazing changed much of the woodland to native grassland [S3] (Colclough 1960, Moore 1970, Adamson and Fox 1982, Benson 1991).

A cool-season dominated woodland was probably maintained by light to moderate stocking, and could have reverted to the original state if stock were removed or grazing was of short duration. However, as grazing continued the reversion became less likely as palatable species disappeared. *Themeda* for example, is considered an 'extinction prone' grass because of its susceptibility to grazing, reliance on seed for regeneration, and inability to form long-term seed banks (O'Connor 1991). An interaction between drought and sustained grazing may also have led to a collapse of perennial grass populations (Hodgekinson and Cooke 1995, Adamson and Fox 1982). The loss of propagules of native species created an asymmetric boundary [B1] preventing a return to initial vegetation composition from cool-season woodland or grassland.

Cool-season native grasslands consisted primarily of perennial grasses and native forbs, and could have been maintained by light grazing. Such sites could switch to cool season woodlands if bare soil was available, *E. albens* seed reached the site, grazing pressure and seed predation was low, and weather was favorable (Clayton-Greene and Ashton 1990), probably a rare occurrence. Gradual expansion of wooded patches into cleared or open areas is the most likely process since dispersal distance is low (Curtis 1990, Clayton Green and Ashton 1990) and recruitment of tree seedlings appears to be highest just outside the driplines of mature seed-bearing trees (Curtis 1990, Windsor 1998). There can be substantial differences in soil properties beneath and between tree

canopies (Chapter 5, Prober *et al.* in review), and a shift between grassland and woodland could have altered understory composition.

Continued grazing and invasion of exotic species caused a further shift towards an understory dominated by exotic species and drought- and grazing-tolerant native species including *Bothriochloa macra* and *Chloris truncata* (Moore 1970). A mixed native-exotic understory was likely maintained under moderate grazing, with periodic heavy grazing during good seasons. The presence of exotic species (mostly annuals) created a second asymmetric boundary [B2] by competing with native perennial species and creating nutrient cycling feedbacks (Wedin 1999). Nutrient enrichment, especially sowing of nitrogen-fixing species and addition of superphosphate fertilizer likely exacerbated this by stimulating growth of exotic annuals to a greater extent than native species (see Chapter 3) and facilitating space pre-emption by annual exotic species.

Soil disturbance (by rabbit activity, for example), continued grazing, and stock camping under trees created patches dominated by noxious weeds. At the Burrendong site, for example, grazing pressure increased in the 1900s, rabbits became abundant, the effects of drought became more pronounced, and the mixed grassland or woodland degraded further (Coulclough 1960). In sites where clearing did not occur but grazing, stock camps, and rabbit activity increased, a "weedy woodland" resulted [S4]. This state was not sustainable, since *E. albens* seedlings compete poorly with exotic weeds (Chapter 3), seedling recruitment is low in sites with non-native understory (Curtis 1990, Cluff and Semple 1994, Windsor 1998), and trees in sites with degraded understory often suffer from dieback and do not produce seed (Curtis 1990, Landsberg and Wylie 1991, Windsor

1998). With the death of mature trees, the weedy woodland will proceed to degraded or mixed pasture.

At Burrendong, erosion control efforts by the Soil Conservation Service in the 1960s returned most of the badly degraded areas to mixed pasture (Colclough 1960) and there was some regeneration of tree seedlings, primarily *Callitris glaucophylla* with some *E. albens*. This dense regeneration is a transitional state [S7], which may head towards a state that does not currently exist [S8]. In the past, intermittent fire would have limited dense stands of cypress pine and maintained eucalypt woodland on better quality soils; however, fire is currently suppressed or highly managed in most woodlands. Yates and Hobbs (1997a) have suggested that continued grazing on badly degraded sites [S6] results in erosion and salinization, shifting the system across another asymmetric boundary and creating a completely unproductive state (not represented in Figure 6.1).

Refining the model: experimental and survey methods

From 1997 to 2001, we conducted a series of experiments and vegetation surveys to refine our S&T model and to test the proposed asymmetry of the boundaries. The primary experiment was a herbivore exclusion study conducted at Burrendong Dam, NSW (see Chapter 5 for a full description of the study area). Briefly, in February 1997 we established a series of 25m by 25m experimental plots with four herbivore exclusion treatments: T1 (control) was unfenced to allow access to all vertebrate herbivores present at the site (domestic stock, kangaroos, and rabbits); T2 (stock fence) excluded sheep and cattle only; T3 (kangaroo fence) excluded domestic stock and kangaroos, and T4 (complete exclosure) excluded all vertebrate herbivores (stock, kangaroos, and rabbits).

In order to assess the effects of clearing and other habitat-related characteristics experimental plots were placed in three habitats (representing different states in Figure 6.1): S2 or S4 woodlands (intact white box canopy), S3 or S5 grasslands (canopy cleared to improve pasture), and S5 or S6 alluvia (high-productivity drainage lines). There were few patches of grassland that fell into the S6 category, so alluvia were considered analogous to highly disturbed and enriched grassland sites (though topographically different) since soils and species composition were similar between very disturbed grasslands and alluvia. The fully factorial habitat-by-treatment design was replicated in four blocks (each a creek watershed), to give 48 experimental plots (details given in Chapter 1).

Within the context of this experimental design we conducted a number of surveys and experiments to address particular aspects of vegetation and soil dynamics. Seed dynamics were assessed, and particular attention was paid to determining the utility of the soil seed bank for restoration purposes (Board 2002). Seedlings of native species were planted in experimental plots to determine the effect of herbivores on seedling growth and survival (Chapter 2). Vegetation composition and diversity were monitored to test how habitat and exclusion of different herbivores would affect woodland understory (Chapters 4 and 5). Finally, soils were sampled in all experimental plots to assess the relationships of habitat, vegetation, and herbivore exclusion to soil properties (Chapters 5 and below).

Additionally, we conducted a controlled greenhouse experiment to investigate the competitive effects of exotic seedlings on native seedlings and the growth responses of native and exotic species to phosphorus enrichment (Chapter 3). Finally, we conducted a

survey of vegetation and soils in woodland remnants in the Burrendong region, including several woodland patches within the Burrendong study site but not included in the herbivory experiment.

i. Seed dynamics

This portion of the study investigated the potential of the seed bank and seed rain to promote vegetation recovery when grazing disturbance was reduced or removed. In terms of the S&T model (Figure 6.1), it specifically addressed T4 and T5, the reversibility of T6, T7, and T8, and the presence of B1.

In October 1998 (spring) and March 1999 (summer) soil cores 5cm in diameter and 5cm deep were extracted from each S3 or S5 grassland and S2 or S4 woodland experimental plot in two of the four blocks used for the main exclosure experiment. Sample points were arranged in a regular grid pattern within each plot (nine points for spring samples and 27 for summer), and samples were bulked in groups of nine to give one bulked sample per experimental plot in spring and three samples in summer. A similar design was used for seed rain using pitfall cups 7cm in diameter and containing propylene glycol, and these were opened for 7 days in each season.

Soil samples were divided into two portions, and one portion was treated with aqueous smoke extract (known to stimulate germination of some native Australian species) while the other was treated with water. Samples were spread in germination trays and grown for 10 weeks under standard greenhouse conditions, and seedlings were counted and identified following germination. Seeds in seed rain samples were counted and identified

under a compound light microscope. A detailed description of experimental methods and data analysis is given in Board (2002).

ii. Seedling survival and herbivory

This portion of the study investigated the effects of herbivore management and habitat on growth and survival of native plant seedlings. In terms of the S&T model, it represented an attempt to reverse T7, induce T4, and overcome B1 and B2 by introducing missing seedlings in addition to managing herbivory.

In April 1998, 20 individuals each of *Eucalyptus albens, Callitris glaucophylla,* and *Themeda australis* were planted in S3/S5 grassland and S2/S4 woodland experimental plots. Survival, growth (height), flowering (for *T. australis*), herbivory events and identity of herbivore, and overgrowth by surrounding vegetation (usually annual exotic species) were recorded approximately monthly until April 1999, with final measurements taken in 2001. Details of the experimental design, sampling, and data analysis are given in Chapter 2.

*iii.*Understory composition

This portion of the study was designed to provide a description of vegetation in woodland, grassland and alluvial sites, and to investigate the response of vegetation to herbivore exclusion. In terms of the S&T model, it provided descriptions of S2, S3, S4, S5, and S6, and tested whether vegetation would move from a more to a less degraded state within four years of reducing grazing pressure (i.e. tested whether B1 or B2 might exist).

In March 1997, we established 16 $1m^2$ quadrats in a regular grid pattern within each experimental plot in the primary study, and randomly selected 10 of these for permanent monitoring. We estimated percent cover for all plant species (as well as total cover and cover of standing dead material) in each quadrat in March 1997, 1998, 1999, and 2001 and in October 1998 and 2000. During each sampling period we also compiled a complete species list for each experimental plot and sampled standing biomass in 12, 7cm diameter clip plots located in a regular grid pattern (biomass samples were bulked for each plot). We analyzed biomass and species richness patterns in relation to habitat and herbivore exclusion (Chapter 4) and tested for changes in species composition and cover of particular species groups with herbivore exclusion (Chapter 5). Details of sampling and analyses are given in Chapters 4 and 5.

iv. Soils

This portion of the study was designed to investigate the relationship of soil parameters to vegetation and to determine whether soil parameters would change with herbivore exclusion. In terms of the S&T model, it provided descriptions of soils in S2-S6 and tested whether soil properties might contribute to creating B2.

In March 1999, we used the soil surface assessment component of the Landscape Function Analysis (LFA) technique (developed to provide landholders with a quick and effective means of assessing soil and pasture quality: Tongway 1994, Appendix 3) to calculate indices of soil infiltration capacity, stability, and nutrient cycling capacity. We measured soil surface characteristics in the permanent $1m^2$ quadrats, and used these measurements to calculate an average value of each index for each experimental plot.

We then used MANOVA to test for differences between habitats and herbivore exclusion treatments. Chapter 5 contains a more detailed description of the sampling methods and data analysis.

In March 2001, we collected 20 soil samples (2cm depth) in each experimental plot using a stratified random sampling technique. Samples were stratified and bulked based on vegetation characteristics surrounding the sample point, to give two samples per experimental plot: for unwooded habitats samples were stratified into annual-dominated and perennial-dominated samples, and for woodlands samples were stratified into below-canopy and open samples. We analyzed soil samples for total carbon, total sulphur, total nitrogen, available nitrogen, available phosphorus, pH, and electrical conductivity. These measurements were used in a PCA to distinguish among habitats and vegetation strata, and a MANOVA to test for effects of habitat and herbivore exclusion treatment (Chapter 5). Finally we used a series of paired t-tests to test for differences in carbon, nitrogen, and phosphorus concentrations between vegetation strata. Because five tests were used for each habitat, we selected an alpha level of 0.01 rather than 0.05.

v. Influence of nutrients on competition between native and exotic seedlings

This portion of the study was designed to test the responses of important native and exotic species to phosphorus enrichment, and to investigate the competitive effects of exotic species on native seedlings. In terms of the S&T model, it tested the potential for phosphorus addition to interact with exotic species invasion to cause T8, T10 and T12 (and potentially to create B2).

The study was conducted in a greenhouse at the University of Alberta between April and October 2000. In the first experiment, seedlings of four native species (*Eucalyptus albens, Themeda australis, Bothriochloa macra,* and *Danthonia racemosa*) and two exotic species (*Echium plantagineum* and *Vulpia bromoides*) were grown under six different soil phosphorus concentrations (0, 5, 10, 15, 30, and 60 ppm) for eight weeks. At the end of the experiment, shoots and roots were collected, dried and weighed. In the second experiment (lasting 6 weeks), seedlings of *Eucalyptus albens* and *Bothriochloa macra* were grown either alone, with a conspecific competitor, or with a seedling of *Echium plantagineum* or *Vulpia bromoides*, and were subjected to a soil phosphorus concentration of either 10ppm or 100ppm. At the end of the experiment, shoots and roots were collected, dried and weighed. We used multiple regression to analyze data from the first experiment, and ANOVA to analyze data from the second experiment. Chapter 3 presents a detailed description of experimental design and data analysis.

iv. Regional context

This portion of the study was intended to provide a larger-scale context for the primary experiments, and to determine what vegetation and soil characteristics appear to be related to "high", "intermediate", and "poor" quality remnant vegetation. In terms of the S&T model, it described vegetation and soils in states S1-S6, and helped determine the role of soils in creating B1 and B2.

In April 2001 eight remnant woodlands located within 200 km of Burrendong Dam were identified, and an additional four patches at the Burrendong site were also sampled. We selected a representative 25m by 25m area within each remnant, and recorded all

species present as well as an index of cover (present, <1%, 1-5%, 5-10%, 10-25%, 25-40%, 40-60%, 60-80% and over 80%). We collected and analyzed soil samples following the same procedure as for the primary experiment. Where available, we also obtained complete species lists for regional remnants (provided by S. Prober, K. Thiele, and G. Tonkin; see also Prober and Thiele 1995).

We classified these additional samples as "good quality" (S1), "intermediate" (S2-S3), or "poor" (S4-S6) based on dominant vegetation (see Appendix 2). Currently ungrazed remnants dominated by native grasses including *Themeda australis, Poa sieberiana* and containing forbs including *Microseris lanceolata* were classed as "good quality" (S1). Remnants with current or recent grazing, vegetation dominated by native species including *Stipa* and *Danthonia* but little or no *T. australis, P. sieberiana*, or *M. lanceolata,* and containing some common exotic species were classified as "intermediate" (S2). Remnants that were either highly disturbed in the past or undergoing heavy current grazing, and that were dominated by exotic species with few or no native grasses were classified as "degraded" (S4-S6 depending on degree of invasion and tree canopy). We conducted MANOVA to test whether soil parameters differed among degradation states.

Evidence for states, transitions, and boundaries: results and discussion

i. Seed dynamics

The soil seed bank and seed rain were both dominated by annual exotic species, in particular annual fescues (*Vulpia bromoides* and *V. myuros*) (Figure 6.2; Board 2002). Seed bank composition was a subset of the standing vegetation in the previous season, but contained a larger proportion of exotic species. Very few native species were found

in either seed bank or seed rain, and no species were recorded that were not present in the above ground vegetation. Only one *Eucalyptus albens* seed was found in the course of the study, and native perennial grasses were not strongly represented. Neither *Themeda australis* nor *Microseris lanceolata* (species considered indicators of high-quality remnant woodland: S. Prober pers. comm.) were found. Although *Poa siberiana* was present in the standing vegetation of some experimental plots, seed was not recorded in the seed bank or seed rain. There was a positive effect of aqueous smoke extract on germination of most species (with the exception of the annual fescues), but both exotic and native species were affected equally. The effect of herbivore exclusion was inconsistent, in part because seed dynamics were assessed only 2 yr after the exclosures were constructed, but also because the plots were relatively small and seed rain was possibly influenced by edge effects.

Most importantly, there was no indication that remnant recovery could be facilitated by seed rain or seed bank. In fact, the seed rain and seed bank will likely be a hindrance to restoration efforts because of the overwhelming exotic component. Species missing from the above-ground vegetation were also missing from the seed rain and seed bank, and given the short-range dispersal of most seeds (with the exception of ruderal weeds), coupled with the fragmented nature of remnant woodland, natural dispersal of desirable seed into degraded remnants is extremely unlikely. It appears that loss of species from remnants is permanent and that the seed dynamics of remnants (S2-S6) are dominated by annual exotic species. It is also possible that seed dynamics in S1 are more strongly influenced by exotic species than is evident in the above-ground vegetation (e.g. Morgan 1998).

These results support the potential existence of B1 (related to species loss) and B2 (related to exotic species dominance). The predominance of exotic species in the seed rain and seed bank and continued fragmentation of woodland remnants could make these boundaries more asymmetric over time. Disturbance in relatively good condition remnants could allow more rapid degradation, and recovery with removal of disturbance would be increasingly difficult once exotic species became established.

ii. Seedling survival and herbivory

Mortality of all three species was greater in cleared (grassland) areas than in woodland areas (Figure 6.3), but growth rates were also greater resulting in a substantial proportion of seedlings reaching escape height when protected from grazing (Chapter 2). For *Themeda australis*, herbivory (by any species) increased mortality, decreased growth, and decreased the probability of flowering and setting seed. However, when protected from grazing up to 54% of individuals were overgrown and killed by surrounding vegetation (annual exotic species). For *Eucalyptus albens* exclusion of stock appeared to be sufficient to allow adequate survival and growth of seedlings, and for *Callitris glaucophylla* exclusion of each herbivore allowed successive increases in growth and survival but rabbits were the most frequent browsers of *Callitris* seedlings.

The seedling transplant experiment found that reduction of herbivory will be essential for remnant recovery once species are established. Excluding different herbivore species will affect resulting vegetation composition, and abundant exotic species could prevent vegetation recovery (i.e. create B2) especially under reduced grazing. Removing stock would allow recovery of *Eucalyptus* and perhaps *Callitris*, but

not *Themeda*. Rabbit control alone would likely promote growth of *Callitris* but not the other two species (this is also evident from a *Callitris* recruitment event that occurred at Burrendong following arrival of myxomatosis and substantial rabbit reduction efforts – Colclough 1960).

The results provide evidence for T1 and suggest that sustained grazing in a good quality remnant could cause a shift across B1. Grazing reduced growth, survival, and seed production of *Themeda*, indicating that extirpation under sustained grazing is possible and replacement of individuals from seed would become increasingly unlikely. However, relatively high survival of all species in fenced plots indicates that re-introduction of species in combination with reduced grazing may allow a shift back across B1. The results also reinforce the role of exotic species in sustaining the asymmetry of B2. In the absence of grazing overgrowth by annual exotic vegetation was the primary cause of mortality (especially for *Themeda*), and thus grazing reduction in invaded sites is unlikely to be effective in promoting seedling establishment and must be combined with some form of weed control. This is a commonly reported problem in similar ecosystems worldwide (Eliason and Allen 1997, Hamilton *et al.* 1999, Brown and Rice 2000, Yates *et al.* 2000), and is a major focus of research efforts in Australia (e.g. the Cooperative Research Centre for Australian Weed Management: http://www.waite.adelaide.edu.au/CRCWMS, Sindel 2000).

iii. Understory composition

Overall, the remnants at Burrendong contained 309 plant species in the understory, 148 exotic and 161 native (Appendix 1). Most of the exotic species were cool-season

annuals. Treeless patches supported a higher proportion of exotic species than woodland patches (S3/S5 grasslands 45%; S5/S6 alluvia 76%; S2/S4 woodlands 25%; Figure 6.4).

There was some response of understory vegetation to fencing treatments, but this response was limited. Native, exotic and total species richness showed no consistent patterns with herbivore exclusion, though there was a tendency for richness to decline in unfenced plots or stock fences during a period of low rainfall (Chapter 4). Standing biomass tended to increase with increasing level of exclosure, and stock and kangaroos appeared to have the largest influence on biomass accumulation (Chapter 4). Species richness was related to total cover and standing biomass, with both native and exotic species showing unimodal responses; however, the overall slopes of the relationships were negative for native species and positive for exotics.

Species composition changed little with fencing, and fencing treatment explained less than 8% of variation in species composition (Chapter 5). There was an increase in native perennial grasses with C3 anatomy in treatments that excluded both stock and kangaroos over the course of the experiment. There was little change in cover of any other native species group, and no species considered typical of high quality white box woodland appeared in plots from which they were initially absent. Exotic perennial forbs and exotic rosette forming forbs showed an increase in cover in fenced plots.

The overall composition indicates that the remnants used in the exclosure experiment fell primarily into S2-S5 categories, though some alluvial sites were very badly invaded and should be considered S6 (Figure 6.1, Figure 6.4). No previously extirpated woodland species appeared during the course of the experiment, indicating that T4 is unlikely without addition of missing species.

There was also some evidence of movement between states within areas bounded by B1 and B2 (shift in native perennial grass cover or exotic species cover with no change in species). However, both native and exotic species responded positively to herbivore exclusion, thus reduction of herbivory alone will not be adequate to overcome the problem of exotic species invasion in woodland remnants, at least within a 4-5 year time frame. Our results raise the concern that fencing in the absence of another form of disturbance may result in reduced native species richness (but not reduced exotic richness) by allowing accumulation of biomass.

In summary, our investigation of understory species composition and response to herbivore exclusion reinforces the presence of B1 (based on species loss) and B2 (based on exotic species invasion). Herbivore management can cause some compositional changes, but cannot move the system across either boundary. In addition, exclusion of domestic stock without reduction of other herbivores (especially kangaroos) is likely to be ineffective.

iv. Soils

Habitats and strata within habitats could be differentiated (though not completely) based on soil parameters (Chapter 5, PCA). The largest difference between strata was seen in S2/S4 woodlands, where canopy samples had higher nutrient levels than open samples (Figure 6.5). A similar trend was evident in S5/S6 alluvia (higher nutrients in annual samples), but the differences were much smaller. S2/S4 generally had higher carbon, nitrogen and sulphur than other habitats, while S3/S5 grasslands had lowest pH, lowest nutrients, and highest electrical conductivity.

The results of paired t-tests are presented in Table 6.2. For S3/S5 grassland samples, there was no difference between annual and perennial samples in any of the properties examined, though most nutrients tended to be slightly higher in perennial samples. In alluvia, total nitrogen and available nitrogen were significantly higher in annual samples. In woodlands, both carbon and total nitrogen were significantly higher in canopy samples. The difference between strata in S2/S4 woodlands was substantial (e.g. carbon; Figure 6.5) indicating that clearing of adult trees could have a large impact on soil properties (soil feedbacks may help maintain states S2 and S3 as separate states, though there is no boundary between them).

Exclusion of herbivores had little impact on soil parameters. There were no differences in soil nutrient concentrations, pH, or electrical conductivity among fencing treatments (Chapter 5). Soil infiltration capacity and stability did not change after two years of treatment; however, soil nutrient cycling capacity improved in all fenced plots (Chapter 5). This was likely due primarily to accumulation of litter and to a lesser extent some increase in perennial plant cover.

Our results show that habitat differences may be related to soils and the soil-vegetation feedback (soil parameters accounted for most of the variation in species composition at the end of the experiment – Chapter 5). Tree clearing could have a major impact on soil processes, reducing the number of microhabitats available in woodland remnants and potentially contributing to species loss and the creation of B1.

Other studies have related soil phosphorus (Cale and Hobbs 1991, Morgan 1998) or soil nitrogen (Prober *et al.* in review) to degree of exotic species invasion in woodland and grassland habitats. Our results showed no strong relationship of nutrients to annual

(mostly exotic) or perennial (mostly native) species groups; however there was some indication that nitrogen was higher in annual patches (a result consistent with Prober *et al.* in review). This result contradicts the common observation that phosphorus addition leads to exotic invasion in Australian woodlands, and does not strongly support the idea that nutrient addition would facilitate invasion and contribute to B2 in the field. However the results of other studies indicate that weed invasion can be facilitated by nutrient addition (see Chapter 3) and that soil-vegetation feedback can maintain high-nutrient annual patches (Vinton and Burke 1995, Wedin 1999).

Herbivore exclusion treatments had little effect on soils (in contrast to the results of Windsor 1998) with the exception of nutrient cycling (driven by litter accumulation). Windsor's study was conducted in very degraded remnants (isolated trees in exotic pasture), and it is possible that de-stocking might facilitate a shift from very degraded (S6) to moderately degraded (S5) condition but will not cause soil changes that would facilitate crossing B2.

v. Influence of nutrients on competition

The two exotic species tested (*Echium plantagineum* and *Vulpia bromoides*) both showed a much stronger growth response to added phosphorus than did any of the native species tested (Chapter 3). In addition, *E. plantagineum* had a much stronger competitive effect on *Eucalyptus albens* than did conspecific competitors (Figure 6.6). *V. bromoides* was less influential as a competitor, but the effect of *Vulpia* in the field appears to be due to its ability to form dense stands and create thatch that smothers competitors and prevents recruitment of other species (Allcock, personal observation; Brown and Rice

2000). There was no interaction between phosphorus level and competitive effect of exotic species (Figure 6.6, Chapter 3).

Phosphorus enrichment encouraged both root and shoot growth of exotic species to a much greater extent than native species (Chapter 3). Alhough there was no interaction between phosphorus level and competitive effect, rapid growth of exotics under enriched conditions could allow them to become established more quickly than native species in the field, and pre-empt space as well as out-competing native species. In addition, the species that was the best competitor (*Echium plantagineum*) is an exotic rosette-forming annual (one of the species groups that showed an increase in cover with herbivore exclusion: Chapter 5) indicating that fencing without some other form of disturbance to reduce exotic species will be ineffective in allowing remnant recovery. These results also support the existence of B2, and suggest that both nutrient enrichment and exotic invasion may contribute to this boundary although their effects are likely additive and not synergistic.

We did not test the effects of nitrogen addition on growth or competition; in light of the results of our soil survey (and Prober *et al.* in review) it appears that nitrogen addition may be more important in the dynamics of woodland vegetation than previously thought. The effects of nitrogen on exotic-native species interactions should be investigated.

vi. Regional context

Species lists for the eight remnants outside the Burrendong area and the four additional remnants at Burrendong are presented in Appendix 2. Remnants that were classified as "good" condition (S1) were dominated by native species including *Themeda*

australis, but there were some exotic species present and all remnants contained weedy patches. Remnants in "intermediate" (S2) condition were again dominated by native species, but were missing some native species present in good condition remnants, and exotic species were more abundant than in good condition remnants. "Poor" condition remnants (S4-6) were dominated by exotic species (primarily forbs) and those native species that were present tended to be disturbance tolerant forbs and grazing tolerant grasses.

The overall MANOVA did not show significant differences in soil characteristics among degradation classes (Pillai trace=0.687, F=1.67, DF=10, 32, p=0.013). However univariate responses showed that available phosphorus, available nitrogen, and total nitrogen were significantly higher in poor condition remnants than in either of the other two degradation classes (Figure 6.7). Carbon differed between canopy and open strata but did not show a relationship to degradation class.

The observed species composition fits well with states S1, S2, and S4 as defined from our literature searches, but also shows that there is variability in composition within each defined state. The results of the soils analyses support the idea that B2 (but not B1) is related to nutrient enrichment/soil degradation, since the largest differences in soil nutrient status were evident between poor and intermediate condition remnants rather than intermediate and good condition remnants. Similar results were found in the Wallatin Catchment in Western Australia by Tongway and Hindley (2000).

The effects of herbivory in remnant woodlands

Our research showed that herbivory influenced soils, seedling survival, biomass, and species composition in remnant white box woodland (but did not affect seed dynamics appreciably). It is evident that management of herbivores will be required to provide momentum to reverse the current trends towards degradation in remnant woodland, but fencing alone will not be sufficient to allow remnant recovery. Stock fencing is the most commonly recommended management option for remnant woodland (e.g Elix and Lambert 1997, Spooner *et al.* 2002); however removing stock alone will not be adequate. While stock do affect species composition, standing biomass, soil nutrient cycling, and *Eucalyptus* seedling survival, we found that species composition did not respond to unless both stock and kangaroos were excluded from experimental plots, and *Themeda australis* seedlings were susceptible to herbivory by all species.

It is evident that changes in herbivory can cause shifts between states within the areas between asymmetric boundaries, and contribute to variation within states (that is, herbivory can roll the "ball" around in the "cup" of the stable state; see introduction). We also have evidence that sustained grazing can cause shifts downward across asymmetric boundaries. This pressure can interact with drought to contribute to population collapse and species loss (Hodgkinson and Cook 1995) or to reductions in species diversity (Chapter 4). However, fencing (even removal of all herbivores) does not appear to allow shifts back across boundaries without other intervention such as replacing extirpated species or controlling exotic species. Herbivore control will be an essential step in managing and restoring remnant white box woodlands, but stock reduction alone will not be effective, and fencing will rarely be effective in isolation.

Conclusions

Figure 6.8 summarizes changes in canopy, understory composition, grazing pressure, and soils associated with grazing and clearing in remnant woodlands. This schematic is a simplified version of the S&T model presented in Figure 6.1: thresholds or asymmetric boundaries are represented by solid lines in Figure 6.8. Sustained grazing causes shifts across a boundary from "good" to "intermediate" condition remnants (due mostly to loss of species in the understory) then subsequently across a second boundary from "intermediate" to "poor" condition remnants (due to dominance by exotic species and changes in soils). In "good" and "intermediate" remnants, tree clearing does not create an asymmetric boundary if a seed source is available (recruitment of canopy species is possible in "good" or "intermediate" grassland); however, once the system has crossed both grazing-related boundaries, tree clearing or death does create a threshold.

The state and transition model appears to be a useful framework to describe the vegetation dynamics of remnant box woodlands. Our observations at Burrendong Dam and in surrounding remnants support the structure of the model in its current form, and (importantly) support both the existence of and the proposed mechanisms behind the two asymmetric boundaries identified in Figures 6.1 and 6.8.

In reality, most remnants contain patches that fall into various states as identified by the S&T model; there is often substantial variation in condition at the sub-remnant scale. The states we have identified are variable, but our data generally support the causes and mechanisms we have outlined for transitions, and the primary objective of the modelling exercise (identification and description of boundary conditions) was successful. The characteristics of the identified states and the management options that flow from the

characteristics of the identified states and the management options that flow from the S&T model can be applied at any scale. The S&T framework would allow for overall management recommendations to be made at the scale of an entire remnant and help identify additional intensive management to be applied to patches within each remnant.

Our research has improved our understanding of woodland vegetation and has provided a conceptual framework upon which to base management decisions; however further research is needed to refine the model and provide a more complete picture of vegetation dynamics. Three aspects, in particular, need to be addressed.

First, it is essential that we understand the role of disturbances other than herbivory in this system. Our results show that native species richness may decline with increasing biomass and that exotic weeds can increase in the absence of disturbance and can cause mortality of native seedlings. In addition, many native species (*Eucalyptus* for example) recruit best on bare soil (e.g. Curtis 1990, Windsor 1998). Fire has been suppressed in woodland remnants since the establishment of European settlements and the effect of burning on remnant vegetation should be investigated.

Second, our study highlights the influence of exotic species on remnant woodlands. It is evident that control of exotic species will be essential for effective restoration of most remnants, and means for achieving this should be investigated. Prescribed burning is an option and is being implemented in some remnants (S. Prober, personal communication), but the frequency, timing, and intensity of burns would greatly affect the management outcome and further information is needed. In addition, the use of intense short-term grazing (including optimal timing, duration, and intensity) to control biomass and exotic species should be studied.

Finally, the role of nutrients (especially nitrogen) in creating and maintaining B2 must be investigated. We have shown that phosphorus enrichment can encourage growth of exotic species over that of native species in a greenhouse experiment, and there are numerous studies from other ecosystems that suggest nutrient enrichment facilitates exotic invasion. However field evidence for the importance of phosphorus in white box woodland is limited, and the response of exotic and native species to additional nitrogen has not been investigated.

Though our understanding of white box woodland vegetation dynamics is not complete, our S&T model framework appears to be sound. Our field observations and experiments support our predictions, have allowed us to refine the model, and have highlighted important areas for which information is lacking. The S&T framework is an efficient and useful way to direct conservation decision making. Most management plans for remnant vegetation contain some sort of decision making tool, frequently using flow-chart or binary key format (e.g. Hobbs and Yates 2000). The S&T framework provides an intuitive, concise, informative, and ecologically-based tool for decision making. For fragmented and highly modified ecosystems such as remnant box woodlands the ability to identify asymmetric management boundaries and possible ways to overcome them will be indispensable in the long term conservation and restoration of these communities (Prober *et al.* 2001).

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Table 6.1: Literature sources used in the construction of the state and transition model for White Box woodlands, including the location and topic of each paper, and the components of the models to which each source applied.

Source	Topic and region	Model
Adamson & Fox (1982)	Vegetation change since European settlement in Australia; causes of rapid vegetation change	B1, T1-T8, S1-S5
Benson (1991)	Vegetation change since European settlement; habitat loss in temperate woodlands	B1, T1-T8, S1-S5
Benson (1999)	Past and present vegetation of NSW, threats, and conservation plans	B1, T1-T8, S1-S5
Clayton-Greene & Ashton (1990)	Composition and dynamics of White box and *Callitris* woodlands in southern NSW	S1-S2, T5
Couclough 1960	Vegetation change and land management at Burrendong Dam	S2-S7, T10, T12, T13
Hodgekinson &Cook (1994)	Perennial grass collapse under grazing in arid rangelands	B1, T1, T4
Lodge *et al.* (1984)	Composition, management, and vegetation change in temperate rangelands in NSW	B1, T1-T8, S1-S5, T9, T11
Logan (1957a,b)	Vegetation change and land management at Burrendong Dam	S2-S7, T10, T12, T13
Lunt (1991)	Conservation and management of grasslands and grassy woodlands in southeastern Australia	B1, T1-T8, S1-S5
Lunt (1995)	Management effects and recommendations in grassy woodlands of southeastern Australia	B1, T1-T8, S1-S5
Moore (1970)	Composition and vegetation change with grazing in temperate grasslands and woodlands of eastern Australia	B1, B2, T1-T8, S1-S5
OConnor (1991)	Extinction in perennial grasslands in Africa	B1, T1, T2, T4
Prober & Thiele (1993)	Conservation status of grassy White Box woodlands in NSW	B1, T1-T8, S1-S5
Prober & Thiele (1995)	Vegetation composition and land use of grassy White Box woodlands	B1, B2, T1-T8, S1-S5
Prober *et al.* in press	Identifying "reference conditions" for White Box woodlands	S1, B1
Prober *et al.* in review	Soil-related restoration barriers in White Box woodlands	B2, S1-S6
Reed (1991)	History of woodland change and conservation in NSW	S1-S6, T1-T11, B1, B2
Wedin (1999)	Vegetation soil feedbacks and nutrient concentrations in North American grasslands	B2
Windsor (1998)	Regeneration of white and yellow box in central west NSW	B2, T9, T11, S4
Yates and Hobbs (1997a, b)	Use of S&T models for understanding vegetation change in Salmon Gum woodlands in WA; threatening processes in Australian temperate woodlands	whole model
Yates *et al.* (2000)	Effects of herbivory and non-native vegetation on woody plant recruitment in Salmon Gum woodlands in WA	B2, T9, T11

Table 6.2: Paired t-tests comparing nutrient concentrations and electrical conductivity in soils from annual- or perennial-dominated strata (alluvia and grasslands) or soils from under or outside tree canopy (woodland).

Variable	Difference	t	p
S5-S6 (Alluvia)			
Carbon	0.698	0.972	0.34
Nitrogen	0.119	2.977	**0.009**
Avail. Phosphorus	8.59	0.902	0.38
Avail. Nitrogen	29.53	4.237	**0.0007**
EC	-26.24	-1.553	0.141
S3/S5 (Grassland)			
Carbon	-0.456	-1.323	0.206
Nitrogen	-0.04	-1.247	0.231
Avail. Phosphorus	-6.995	-0.94	0.359
Avail. Nitrogen	-11.19	-2.500	0.0359
EC	-45.35	-2.855	**0.012**
S2/S4 (Woodland)			
Carbon	5.67	7.766	**<0.0001**
Nitrogen	0.228	4.369	**0.0006**
Avail. Phosphorus	9.20	0.953	0.356
Avail. Nitrogen	8.60	1.144	0.169
EC	-34.906	-1.983	0.066

Figure 6.1: State and transition model for vegetation change in white box woodland (Figure 6.1a). Boxes represent vegetation states; arrows indicate transitions. Dashed boxes are transient states that will move to another state without perturbation. Heavy curved lines indicate asymmetric boundary conditions. Figure 6.1b presents the catalogue of states and transitions for the diagram in 6.1a.

Figure 6.1a

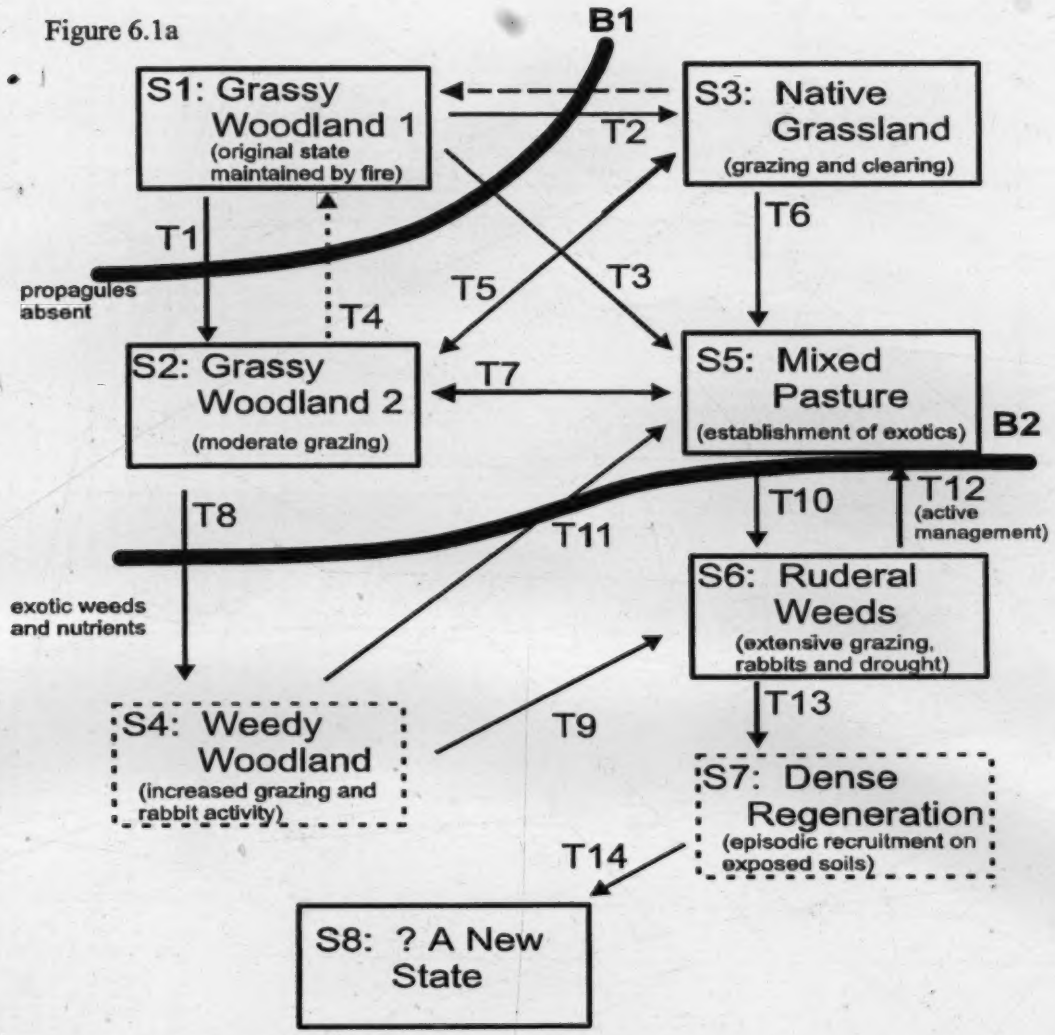
B1
S1: Grassy Woodland 1
(original state maintained by fire)
S3: Native Grassland
(grazing and clearing)
T2
T1
T6
propagules absent
T5
T3
T4
S2: Grassy Woodland 2
(moderate grazing)
T7
S5: Mixed Pasture
(establishment of exotics)
B2
T8
T10
T12
(active management)
T11
exotic weeds and nutrients
S6: Ruderal Weeds
(extensive grazing, rabbits and drought)
T13
S4: Weedy Woodland
(increased grazing and rabbit activity)
T9
S7: Dense Regeneration
(episodic recruitment on exposed soils)
T14
S8: ? A New State

Figure 6.1b

States

S1: pristine woodland – white box canopy and tall grass/forb understory. Maintained by fire and light grazing, and perhaps competition for water.

S2: grazed woodland – white box canopy and short grass understory. Maintained by stock grazing.

S3: native grassland – canopy cleared; grassland of short native species. Maintained by stock grazing.

S4: weedy woodland – transient state. Canopy dying, not regenerating. Understory of invasive weeds.

S5: mixed pasture – canopy cleared, sown pasture species, invasive species, and some less palatable native grasses.

S6: ruderal weeds – badly degraded by overgrazing, no perennial cover. Unpalatable weeds dominate.

S7: dense regeneration – transient state. Primarily *Callitris glaucophylla,* dense even aged stands.

S8: not yet observed at Burrendong. Outcome of aging and self-thinning in S7. Perhaps *C. glaucophylla* forest?

Transitions

T1: grazing of pristine woodland causes reduction or loss of grazing sensitive species and shift to dominance of short grasses.

T2: grazing and clearing removes trees and causes shift to dominance of short grasses; may be reversible early in transition (see T4).

T3: concurrent clearing, grazing, fertilization, and introduction of exotics move pristine woodland directly to mixed pasture.

T4: removal of grazing early in transition from S1 to S2 may permit recovery to S1, but T4 is very unlikely.

T5: recruitment of trees into native grassland, a rare event, or clearing of trees in native woodland.

T6: addition of fertilizer, sown pasture species, and invasive exotic species moves native grassland to mixed grassland.

T7: tree clearing, addition of fertilizer and pasture species, and invasion of exotic species move S2 to S5. Recruitment or planting of trees in S5 moves to S2 (rare).

T8: fertilization, stock camps, and invasion of noxious weeds move S2 to S4.

T9: tree death moves S4 to S6.

T10: continued heavy grazing, erosion, and invasion of noxious weeds moves S5 to S6.

T11: tree death moves S4 to S5.

T12: prompt management such as de-stocking and rabbit control (seen at Burrendong in 1960's) can return S6 to S5.

T13: management attempts to move from S6 to S5 can also result in transition to S7 if propagules available (seen at Burrendong)

T14: growth and self-thinning of S7 creates S8, a previously unrecorded state for woodlands in the Burrendong area.

Boundaries

B1: Grazing causes local extinction of sensitive species and eliminates kangaroo grass. Removal of grazing does not allow return to S1 because of extinction events and loss of propagules.

B2: Addition of nutrients (phosphate), introduction of pasture species, and invasion of exotic weeds mediated by grazing and increased nutrients alters understory composition. Reduction of grazing will not allow native plants to eliminate exotic species and a return from S4 or S5 to S2 or S3 is prevented.

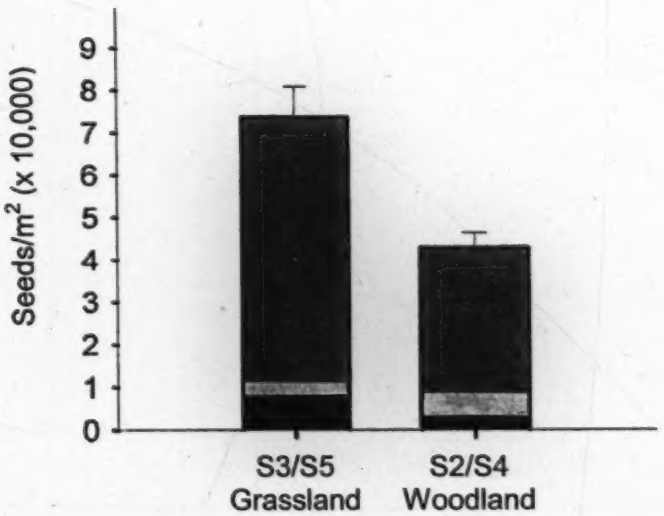

Figure 6.2: Total seeds per m^2 (+ SE) in the soil seed bank at Burrendong Dam divided into exotic (dark grey), native (light grey), and unknown (black) origin. Data are classified based on vegetation state or habitat (grassland=S3 or S5, woodland=S2 or S4). Figure reproduced with permission from Board (2002).

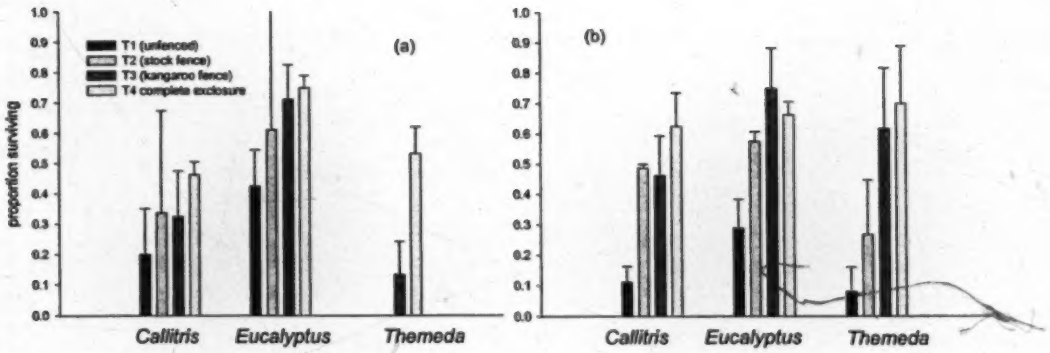

Figure 6.3: Survival +/- SE after 3 years of *Callitris glaucophylla, Eucalyptus albens,* and *Themeda australis* seedlings planted in four herbivore exclusion treatments in a) grassland (S3 or S5) and b) woodland (S2 or S4) habitats.

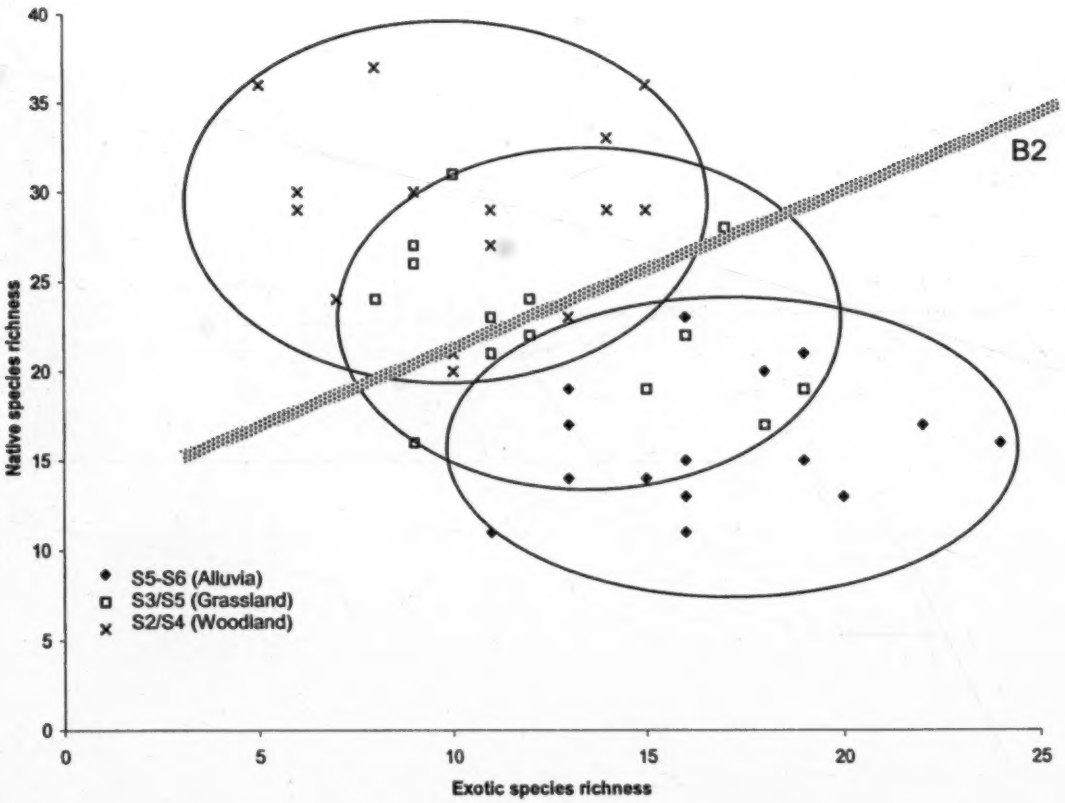

Figure 6.4: Relationship of native species richness to exotic species richness in three habitats in 25m by 25m experimental plots in March 2001. Ellipses represent groups of states (woodland S2 or S4, grassland S3 or S5, alluvia S5 or S6; see figure legend). The diagonal line represents the approximate location of B2 from Figure 6.1.

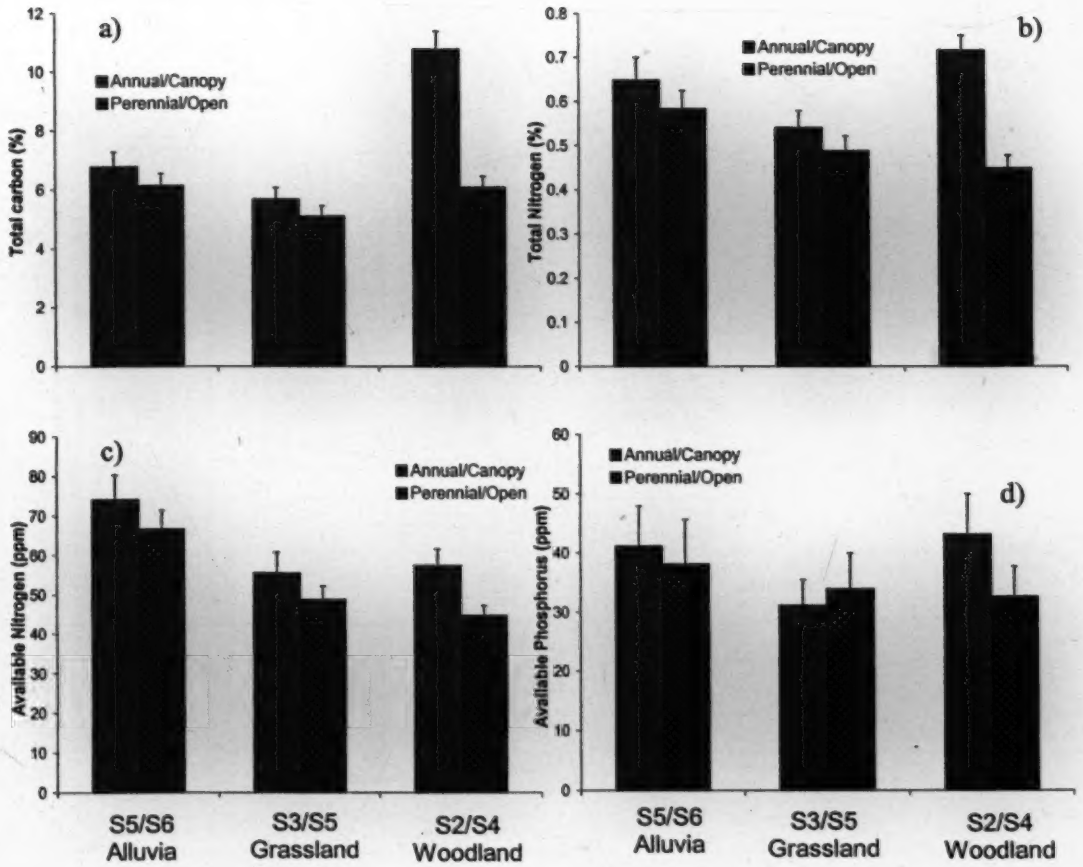

Figure 6.5: Soil nutrient concentrations (+/- SE) in Alluvia (S5-6) Grassland (S3 or S5) and Woodland (S2 or S4) plots in annual and perennial patches (treeless habitats) or canopy and open patches (woodland). Panels are a) total carbon, b) total nitrogen, c) available nitrogen, and d) available phosphorus.

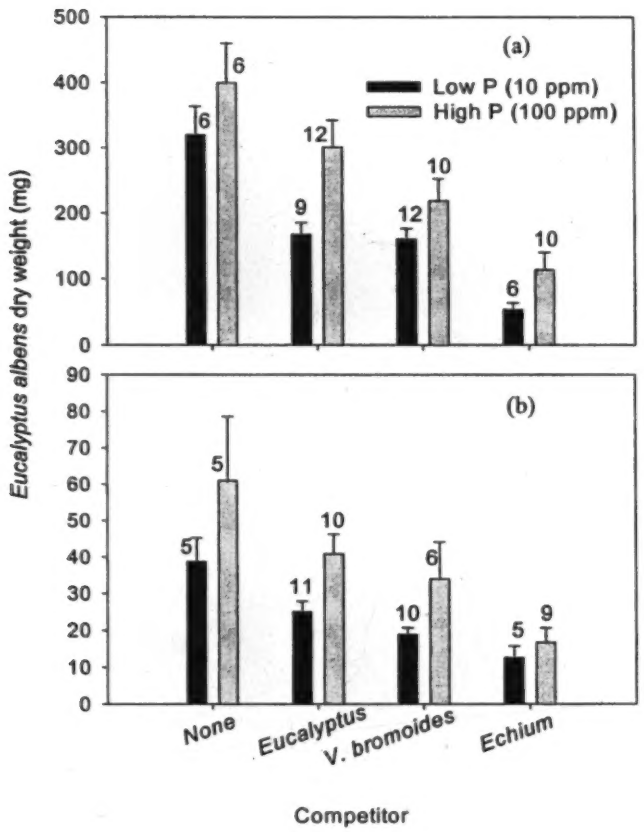

Figure 6.6: Effects of phosphorus on growth and competition of *Eucalyptus* and two exotic species (*Vulpia bromoides* and *Echium plantagineum*). Panels a (shoots) and b (roots) show the competitive effect of exotic species and conspecifics on growth of *Eucalyptus albens* at two phosphorus concentrations. Numbers above the bars represent sample size.

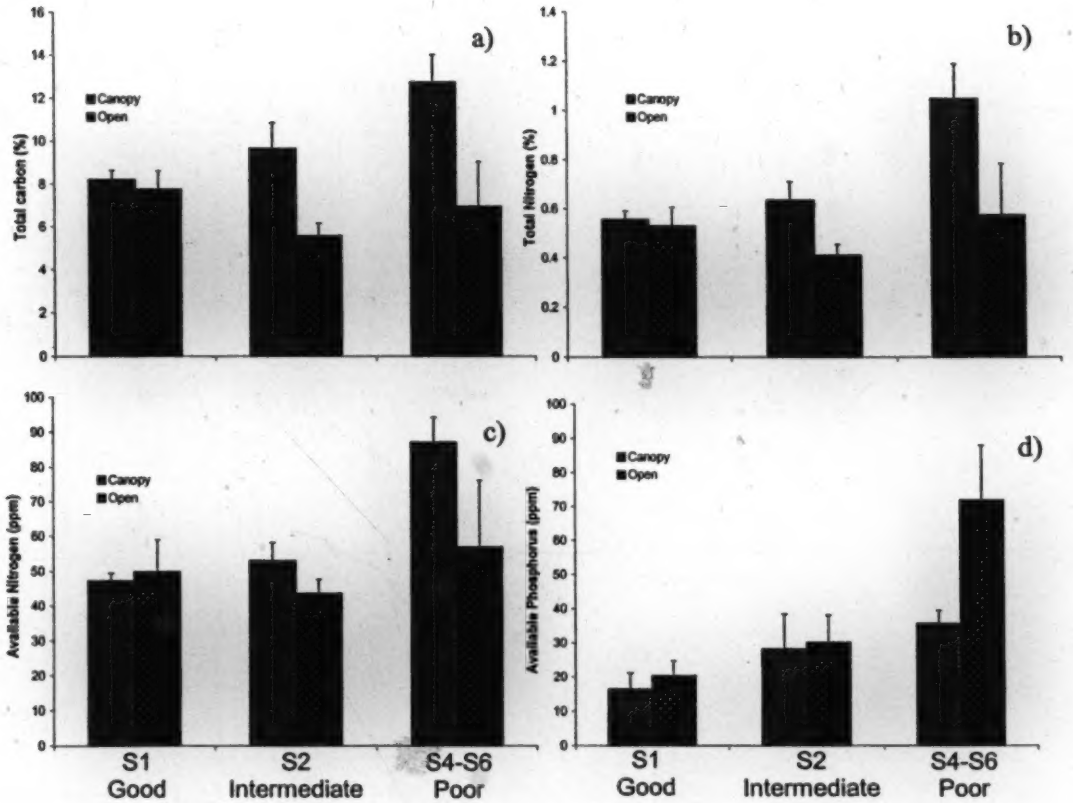

Figure 6.7: Nutrient concentrations (+/- SE) in remnants sampled within 200 km of Burrendong. Remnants were classified into condition states (Good – S1, Intermediate – S2, and Poor – S4-6) based on vegetation composition and land use. Panel a) total carbon, b) total nitrogen, c) available nitrogen, and d) available phosphorus.

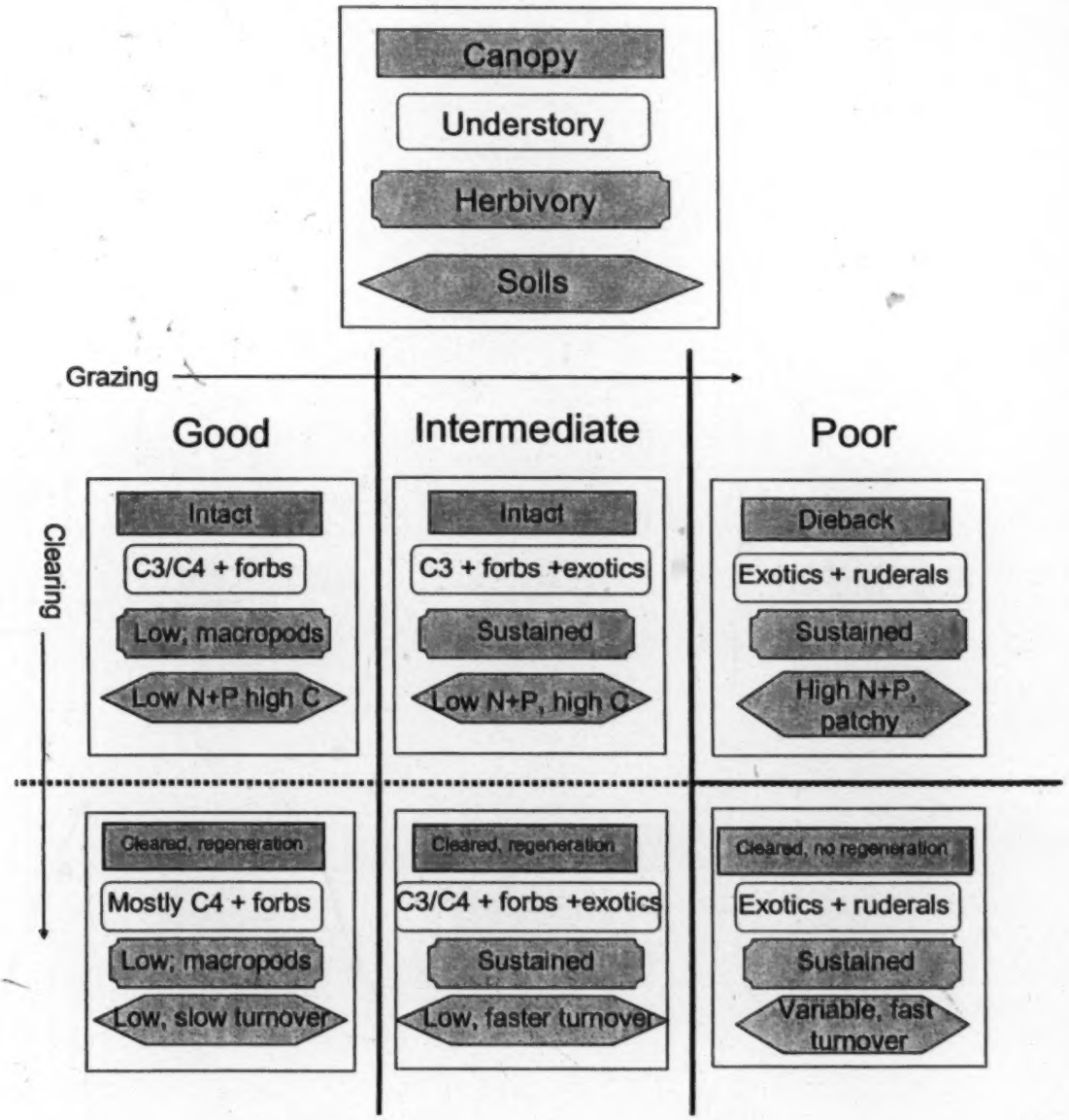

Figure 6.8: Summary of changes in canopy, understory vegetation, herbivory/grazing, and soils associated with clearing and grazing disturbance in white box woodlands. Dashed lines indicate reversible boundaries between vegetation states; solid lines represent asymmetric boundaries or irreversible thresholds between states.

Chapter 7

General Discussion

Experiments in Ecology

Ecological communities are complex, and studies attempting to understand the mechanisms at work in ecosystems must be designed carefully and at an appropriate scale (Levin 1992). A scientific research program in which perceptions (models) of ecological systems produce hypotheses that can be tested experimentally (e.g. Underwood 1997) is the most powerful way to increase our understanding of mechanisms. However there is a tradeoff between realism and precision of the results (e.g. Shindler 1998), creating a continuum of experimental styles ranging from the large-scale ecological experiment to investigating mechanisms separately using microcosms or computer modelling excercises (Lawton 1995). In any investigation an increase in the scale and inclusiveness of the experiment comes at the expense of confidence in the conclusions, as larger spatial and temporal scale means less control over experimental conditions and lower replication (e.g. Carpenter *et al.*1995). Combining large and small scale experiments in a research program may help overcome this.

It has been argued that community ecology is inherently contingent, and that results of community studies can never be generalized because of the complexity of interactions (Lawton 1999). This implies that the reductionist approach would be preferable to the large-scale experimental approach. However, the following statement (attributed to John W. Tukey) applies here: "far better an approximate answer to the right question, which is often vague, than an exact answer to the wrong question, which can always be made

precise". While controlled small-scale experiments allow for easy manipulation of experimental conditions and increase the degree of replication, they are limited in size and complexity (Lawton 1995).

The complexity of interactions in an ecosystem may produce 'emergent properties' that cannot be understood by testing factors individually, and some factors are too large to be included in controlled microcosm or laboratory studies (Carpenter *et al.* 1995, Schindler 1998). At least as important is the consideration that land management and conservation are conducted at the scale of the community or ecosystem; for ecology to inform management (e.g. Carpenter 1996) it is necessary for ecological experiments to be conducted at a large scale.

Exclosure studies

Exclusion studies are frequently used as a powerful means to investigate the role of herbivores in directing the dynamics of plant communities (see Chapter 5). In terms of increasing our understanding the effects of herbivory on diversity, productivity, and resilience of plant communities, exclusion experiments are useful from an ecological, agronomic/economic, and land management perspective. Well designed experiments have a greater potential to determine mechanism than do studies of pattern alone, and thus may provide results which are more widely generalizable (Lawton 1999).

However, there are limitations to this approach. Exclusion of an herbivore and monitoring of the resultant vegetation change is not equivalent to addition of an herbivore, since responses of vegetation are often asymmetric; thus it is difficult to precisely determine the ecological role of herbivores in structuring a plant community. In

addition, many studies are conducted and sampled on inappropriate spatial or temporal scales or have limited replication (Stohlgren *et al.* 1998). In particular, experiments intending to identify multiple state dynamics require large enough experimental plots and long enough time frame to identify stable vegetation states and the boundaries between them (Petraitis and Latham 1998).

Use of Models

It is impossible to design and implement an ecological experiment that is ideal in scale, scope, and rigour: there will always be a tradeoff between generality and precision. A potential solution to this problem is to use formal conceptualizations, or models (*sensu* Underwood 1997) of the ecosystem of interest to generate testable hypotheses. Then, a combination of approaches including observational studies, large scale experimentation, and controlled smaller-scale experiments can be applied to refine the conceptual model of the ecosystem. This approach to the scientific research program may make it possible to begin to draw general conclusions about ecological mechanisms. Some of the limitations of ecosystem-scale studies could be largely overcome by strategic use of replicated experiments at other scales; a combination of experimental/modelling approaches are needed to bridge space and time in studies of community dynamics.

Future research in white box woodlands

I have attempted to apply the scientific approach described above in my study of vegetation dynamics in white box woodland by incorporating regional surveys, intermediate scale field experiments, and controlled laboratory experiments. The research

at Burrendong Dam and the surrounding region has improved our understanding of woodland vegetation, the role of herbivory, and the potential for grazing-induced asymmetric boundaries in communities other than semi-arid rangelands. It has also provided a conceptual framework upon which to base management decisions for box woodlands in southeastern Australia, and is a springboard for further investigations.

First, it is essential that we understand the role of disturbances other than herbivory in this system. Fire has been suppressed in woodland remnants since the establishment of European settlements and the effect of burning on remnant vegetation should be investigated. Second, the Burrendong study highlights the importance of exotic species in remnant woodlands. Control of exotic species will be essential for effective restoration of most remnants, and means for achieving this should be investigated. Prescribed burning is an option, but the frequency, timing, and intensity of burns would greatly affect the management outcome and further information is needed. Third, the role of nutrients (especially nitrogen and phosphorus) in creating and maintaining asymmetric boundaries in the field must be investigated. Phosphorus enrichment can encourage growth of exotic species over that of native species in a greenhouse environment. However field evidence for the importance of phosphorus in white box woodland is limited, and the response of exotic and native species to additional nitrogen has not been investigated. Fourth, vegetation responses to fencing and other management actions should be investigated at larger spatial scales; for example, the effects of management initiatives on whole remnants should be monitored (e.g. Spooner *et al.* 2002; Prober, personal communication). Finally, the long-term dynamics of vegetation in response to herbivore exclusion must be monitored. My research provides an understanding of

vegetation change in the four years following herbivore management and gives evidence that stable states and asymmetric boundaries do exist in White Box woodlands. However vegetation change may not always be evident within five years of treatment (e.g. Collins *et al.* 1998), and assessment of vegetation change at Burrendong after a decade or more of treatment would be invaluable.

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Appendix 1: Species list, origin, growth form, and *a priori* species group for understory species in the experimental plots at Burrendong Dam NSW. (A=annual, P=perennial, B=biennial). Nomenclature after Hardin (1990-1993), The Flora of New South Wales.

Species	Family	Life history	Growth form	C pathway	Group
Exotic species					
Tetragonia microptera	Aizoaceae	A	forb	N/A	eafl
Zaleya galericulata	Aizoaceae	P	forb	N/A	epf
Amaranthus hybridus	Amaranthecaceae	A	forb	N/A	eaft
Ciclospermum leptophyllum	Apiaceae	A	forb	N/A	eaft
Gomphocarpus fruticosus	Asclepiadaceae	P	forb	N/A	epf
Arctotheca calendula	Asteraceae	A	forb	N/A	eafl
Hedypnois rhagodioliodes	Asteraceae	A	forb	N/A	eafl
Solvia stolonifera	Asteraceae	A	forb	N/A	eafl
Chondrilla juncea	Asteraceae	A	forb	N/A	eafr
Hypochaeris glabra	Asteraceae	A	forb	N/A	eafr
Leodonton taraxicoides	Asteraceae	A	forb	N/A	eafr
Conyza bonariensis	Asteraceae	A	forb	N/A	eaft
Conyza canadensis	Asteraceae	A	forb	N/A	eaft
Dittrichia graveolens	Asteraceae	A	forb	N/A	eaft
Erigeron karvinskianus	Asteraceae	A	forb	N/A	eaft
Gnaphalium coarctatum	Asteraceae	A	forb	N/A	eaft
Lactuca saligna	Asteraceae	A	forb	N/A	eaft
Lactuca serriola	Asteraceae	A	forb	N/A	eaft
Sonchus asper	Asteraceae	A	forb	N/A	eaft
Sonchus oleraceus	Asteraceae	A	forb	N/A	eaft
Tolpis umbellata	Asteraceae	A	forb	N/A	eaft
Xanthium spinosum	Asteraceae	A	forb	N/A	eaft
Hypochaeris radicans	Asteraceae	P	forb	N/A	epf
Carthamus lanatus	Asteraceae	A	forb	N/A	thist
Carduus tenuiflorus	Asteraceae	A	forb	N/A	thist
Centaurea calcitrapa	Asteraceae	A	forb	N/A	thist
Centaurea melitensis	Asteraceae	A	forb	N/A	thist
Cirsium vulgare	Asteraceae	A	forb	N/A	thist
Onopordium acanthium	Asteraceae	A	forb	N/A	thist
Silybum marianum	Asteraceae	B	forb	N/A	thist
Bidens pilosa	Asteraceae	A	forb	N/A	eaft
Echium plantagineum	Boraginaceae	A	forb	N/A	eafr
Heliotropium amplexicaule	Boraginaceae	A	forb	N/A	eafr
Heliotropium asperrimum	Boraginaceae	A	forb	N/A	eafr
Heliotropium europaeum	Boraginaceae	A	forb	N/A	eafr
Amsinckia intermedia	Boraginaceae	A	forb	N/A	eaft
Capsella bursa-pastoris	Brassicaceae	A	forb	N/A	eafl
Brassica nigra	Brassicaceae	A	forb	N/A	eaft
Sisymbrium sp. A	Brassicaceae	A	forb	N/A	eaft
Sisymbrium officianale	Brassicaceae	A	forb	N/A	eaft
Sisymbrium orientale	Brassicaceae	A	forb	N/A	eaft
Opuntia aurantica	Cactaceae	P	forb	N/A	epf
Opuntia stricta	Cactaceae	P	forb	N/A	epf
Arenaria serpyfolia	Caryophyllaceae	A	forb	N/A	eafl
Cerastium glomeratum	Caryophyllaceae	A	forb	N/A	eafl

Species	Family	Life history	Growth form	C pathway	Group
Paronycha brasiliana	Caryophyllaceae	A	forb	N/A	eafl
Polycarpon tetraphyllum	Caryophyllaceae	A	forb	N/A	eafl
Stellaria media	Caryophyllaceae	A	forb	N/A	eafl
Petrorhagia nanteuilii	Caryophyllaceae	A	forb	N/A	eaft
Silene gallica	Caryophyllaceae	A	forb	N/A	eaft
Silene nocturna	Caryophyllaceae	A	forb	N/A	eaft
Chenopodium glaucum	Chenopodiaceae	A	forb	N/A	eafl
Chenopodium murale	Chenopodiaceae	A	forb	N/A	eafl
Chenopodium album	Chenopodiaceae	A	forb	N/A	eaft
Hypericum perforatum	Clusiaceae	P	forb	N/A	epf
Citrullus lanatus	Cucurbitaceae	A	forb	N/A	eafl
Cucumis myriocarpus	Cucurbitaceae	A	forb	N/A	eafl
Cyperus eragrostis	Cyperaceae	P	graminoid	N/A	epg
Medicago arabica	Fabaceae	A	forb	N/A	eal
Medicago spp.	Fabaceae	A	forb	N/A	eal
Medicago minima	Fabaceae	A	forb	N/A	eal
medicago polymorpha	Fabaceae	A	forb	N/A	eal
Medicago truncatula	Fabaceae	A	forb	N/A	eal
Trifolium angustifolium	Fabaceae	A	forb	N/A	eal
Trifolium arvensis	Fabaceae	A	forb	N/A	eal
Trifolium campestre	Fabaceae	A	forb	N/A	eal
Trifolium cernuum	Fabaceae	A	forb	N/A	eal
Trifolium dubium	Fabaceae	A	forb	N/A	eal
Trifolium spp.	Fabaceae	A	forb	N/A	eal
Trifolium glomeratum	Fabaceae	A	forb	N/A	eal
Trifolium scabrum	Fabaceae	A	forb	N/A	eal
Trifolium striatum	Fabaceae	A	forb	N/A	eal
Trifolium subterranium	Fabaceae	A	forb	N/A	eal
Centauria tenuior	Gentianaceae	A	forb	N/A	eaft
Geranium molle	Geraniaceae	A	forb	N/A	eafl
Erodium cicutarium	Geraniaceae	A	forb	N/A	eafr
Erodium moschatum	Geraniaceae	A	forb	N/A	eafr
Romulea rosea	Iridaceae	P	forb	N/A	epf
Juncus bufonus	Juncaceae	A	graminoid	N/A	eag
Juncus homalocaulis	Juncaceae	P	graminoid	N/A	epg
Lamium amplexicaule	lamiaceae	A	forb	N/A	eaft
Stachys arvensis	Lamiaceae	A	forb	N/A	eaft
Marrubium vulgare	Lamiaceae	P	forb	N/A	epf
Salvia verbenaca	Lamiaceae	P	forb	N/A	epf
Linum trigynum	Linaceae	A	forb	N/A	eaft
Modiola caroliniana	Malvaceae	A	forb	N/A	eafl
Malva parviflora	Malvaceae	A	forb	N/A	eaft
Ibicella lutea	Martyniaceae	A	forb	N/A	eafl
Proboscida louisianica	Martyniaceae	A	forb	N/A	eafl
Oxalis corniculata	Oxalidaceae	P	forb	N/A	epf
Argemone ochroleuca	Papaveraceae	A	forb	N/A	eaft
Papaver dubium	Papaveraceae	A	forb	N/A	eaft
Papaver somniferum	Papaveraceae	A	forb	N/A	eaft
Aira caryophylla	Poaceae	A	grass	C3	eag

Species	Family	Life history	Growth form	C pathway	Group
Avena barbata	Poaceae	A	grass	C3	eag
Avena fatua	Poaceae	A	grass	C3	eag
Briza minor	Poaceae	A	grass	C3	eag
Bromus alopecuros	Poaceae	A	grass	C3	eag
Bromus brevis	Poaceae	A	grass	C3	eag
Bromus catharticus	Poaceae	A	grass	C3	eag
Bromus diandrus	Poaceae	A	grass	C3	eag
Bromus hordeaceus	Poaceae	A	grass	C3	eag
Bromus madrietensis	Poaceae	A	grass	C3	eag
Bromus molliformis	Poaceae	A	grass	C3	eag
Bromus spp.	Poaceae	A	grass	C3	eag
Bromus racemosus	Poaceae	A	grass	C3	eag
Bromus rubens	Poaceae	A	grass	C3	eag
Digitaria sanguinalis	Poaceae	A	grass	C4	eag
Eragrostis cilliensis	Poaceae	A	grass	C4	eag
Hordeum leporinum	Poaceae	A	grass	C3	eag
Lamarckia aurea	Poaceae	A	grass	C3	eag
Lolium rigidum	Poaceae	A	grass	C3	eag
Poa annua	Poaceae	A	grass	C3	eag
Rostraria cristata	Poaceae	A	grass	C3	eag
Vulpia bromoides	Poaceae	A	grass	C3	eag
Vulpia cilliata	Poaceae	A	grass	C3	eag
Vulpia murale	Poaceae	A	grass	C3	eag
Vulpia myros	Poaceae	A	grass	C3	eag
Vulpia spp	Poaceae	A	grass	C3	eag
Cynodon dactylon	Poaceae	P	grass	C4	epg
Paspalum dilatum	Poaceae	P	grass	C4	epg
Poa pratensis	Poaceae	P	grass	C3	epg
Setaria gracilis	Poaceae	P	grass	C4	epg
Eragrostis pilosa	Poaceae	A	grass	C4	nag
Persicaria prostrata	Polygonaceae	A	forb	N/A	eafl
Polygonum arenastrum	Polygonaceae	P	forb	N/A	epf
Polygonum aviculare	Polygonaceae	P	forb	N/A	epf
Polygonum patulum	Polygonaceae	A	forb	N/A	epf
Rumex crispus	Polygonaceae	P	forb	N/A	epf
Portulaca oleracea	Portulaceae	A	forb	N/A	eafl
Anagallis arvensis	Primulaceae	A	forb	N/A	eafl
Reseda luteola	Resedaceae	A	forb	N/A	eaft
Sherardia arvensis	Rubiaceae	A	forb	N/A	eafl
Gallium divaricatum	Rubiaceae	A	forb	N/A	eaft
Gallium murale	Rubiaceae	A	forb	N/A	eaft
Kikxia elatine	Scrophulariaceae	A	forb	N/A	eafl
Veronica arvensis	Scrophulariaceae	A	forb	N/A	eafl
Verbascum virgatum	Scrophulariaceae	B	forb	N/A	eafr
Linaria pelisseriana	Scrophulariaceae	A	forb	N/A	eaft
Misopates orontium	Scrophulariaceae	A	forb	N/A	eaft
Orobanche minor	Scrophulariaceae	A	forb	N/A	eaft
Parentucillia latifolia	Scrophulariaceae	A	forb	N/A	eaft
Datura stramonium	Solanaceae	A	forb	N/A	eaft

Species	Family	Life history	Growth form	C pathway	Group
Solanum cinereum	Solanaceae	A	forb	N/A	eaft
Solanum nigrum	Solanaceae	A	forb	N/A	eaft
Urtica urens	Urticaceae	A	forb	N/A	eaft
Verbena bonariensis	Verbenaceae	P	forb	N/A	epf
Tribulus terrestris	Zygophyllaceae	A	forb	N/A	eafl
Native species					
Ptilotus lanatus	Amaranthacaceae	P	forb	N/A	npfdt
Alternanthera denticulata	Amaranthecaceae	A	forb	N/A	naf
Alternanthera nana	Amaranthecaceae	A	forb	N/A	naf
Arthropodium minus	Anthericaceae	P	moncot forb	N/A	npfm
Dichopogon fimbriatus	Anthericaceae	P	moncot forb	N/A	npfm
Tricoryne eliator	Anthericaceae	P	moncot forb	N/A	npfm
Daucus glochidiatus	Apiaceae	A	forb	N/A	naf
Hydrocotyle laxiflora	Apiaceae	P	forb	N/A	npfdl
Bulbine bulbosa	Asphodelaceae	P	forb	N/A	npfm
Bracteantha viscosa	Asteraceae	A	forb	N/A	naf
Calotis erimaea?	Asteraceae	A	forb	N/A	naf
Calotis lappulacea	Asteraceae	P	forb	N/A	naf
Centipida minima	Asteraceae	A	forb	N/A	naf
Cotula australis	Asteraceae	A	forb	N/A	naf
Gnaphalium sphaericum	Asteraceae	A	forb	N/A	naf
Isoetopsis graminifolia	Asteraceae	A	forb	N/A	naf
Siggesbeckia australiensis	Asteraceae	A	forb	N/A	naf
Stuartina muelleri	Asteraceae	A	forb	N/A	naf
Triptolodiscus pygmaeus	Asteraceae	A	forb	N/A	naf
Cymbonotus lawsonianus	Asteraceae	P	forb	N/A	npfdl
Solenogyne belloides	Asteraceae	P	forb	N/A	npfdl
Solenogyne dominii	Asteraceae	P	forb	N/A	npfdl
Senecio hispidulus	Asteraceae	P	forb	N/A	npfdt
Senecio quadridentatus	Asteraceae	P	forb	N/A	npfdt
Vittadinia cuneata	Asteraceae	P	forb	N/A	npfdt
Vittadinia muelleri	Asteraceae	P	forb	N/A	npfdt
Gnaphalium involucratum	Asteraceae	A	forb	N/A	naf
Pandorea pandorana	Bignoniaceae	P	vine	N/A	nshrub
Cynoglossum australe	Boraginaceae	A	forb	N/A	naf
Mysotis australis	Boraginaceae	A	forb	N/A	naf
Lepidium pseudohysopifolium	Brassicaceae	A	forb	N/A	naf
Sisymbrium irio	Brassicaceae	A	forb	N/A	naf
Wahlenbergia gracilienta	Campanulaceae	A	forb	N/A	naf
Wahlenbergia communis	Campanulaceae	P	forb	N/A	npfdt
Wahlenbergia luteola	Campanulaceae	P	forb	N/A	npfdt
Wahlenbergia stricta	Campanulaceae	P	forb	N/A	npfdt
Gypsophila australis	Caryophyllaceae	A	forb	N/A	naf
Chenopodium pumilio	Chenopodiaceae	A	forb	N/A	naf
Einedia hastata	Chenopodiaceae	P	forb	N/A	npfdt
Einnedia nutans	Chenopodiaceae	P	forb	N/A	npfdt
Einedia polygonoides	Chenopodiaceae	P	forb	N/A	npfdt
Maireana enchylaeinoides	Chenopodiaceae	P	forb	N/A	nshrub

Species	Family	Life history	Growth form	C pathway	Group
Maireana spp.	Chenopodiaceae	P	forb	N/A	nshrub
Sclerolaena birchii	Chenopodiaceae	P	forb	N/A	nshrub
Hypericum gramineum	Clusiaceae	P	forb	N/A	npfdt
Wurmbea biglandulosa	Colchicaceae	P	forb	N/A	npfm
Convulvulus erubescens	Convulvulaceae	P	forb	N/A	npfdl
Dichondra repens/A	Convulvulaceae	P	forb	N/A	npfdl
Crassula colorata	Crassulaceae	A	forb	N/A	naf
Crassula sieberiana	Crassulaceae	A	forb	N/A	naf
Shoenus apogon	Cyperaceae	A	graminoid	N/A	nag
Carex appressa	Cyperaceae	P	graminoid	N/A	npgm
Carex breviculmis	Cyperaceae	P	graminoid	N/A	npgm
Carex incomitata	Cyperaceae	P	graminoid	N/A	npgm
Carex inversa	Cyperaceae	P	graminoid	N/A	npgm
Lepidosperma laterale	Cyperaceae	P	graminoid	N/A	npgm
Scleria mackaviensis	Cyperaceae	P	graminoid	N/A	npgm
Hibbertia acicularis	Dilleniaceae	P	shrub	N/A	nshrub
Hibbertia obtusifolia	Dilleniaceae	P	shrub	N/A	nshrub
Lissanthe strigosa	Epacridaceae	P	shrub	N/A	nshrub
Chamaecyce drummondii	Euphorbiaceae	P	forb	N/A	npfdl
Trigonella suavissima	Fabaceae	A	forb	N/A	naf
Desmodium varians	Fabaceae	P	forb	N/A	npfdl
Glycine clandestina	Fabaceae	P	forb	N/A	npfdl
Glycine tabacina	Fabaceae	P	forb	N/A	npfdl
Desmodium brachypodium	Fabaceae	P	forb	N/A	npfdt
Senna barclayana	Fabaceae	P	forb	N/A	npfdt
Swainsona galegifolia	Fabaceae	P	forb	N/A	npfdt
Dillwynia juniperina	Fabaceae	P	forb	N/A	nshrub
Sebaea ovata	Gentianaceae	A	forb	N/A	naf
Erodium crinitum	Geraniaceae	A	forb	N/A	naf
Geranium retrorsum	Geraniaceae	P	forb	N/A	npfdt
Geranium solanderi	Geraniaceae	P	forb	N/A	npfdt
Goodenia hederacea	Goodeniaceae	P	forb	N/A	npfdl
Goodenia pinnatifida	Goodeniaceae	A	forb	N/A	npfdl
Gonocarpus elatus	Haloragaceae	P	forb	N/A	npfdt
Haloragis heterophylla	Haloragaceae	P	forb	N/A	npfdt
Hypoxis glabella	Hypoxidaceae	P	forb	N/A	npfm
Juncus australis	Juncaceae	P	graminoid	N/A	npgm
Juncus spp.	Juncaceae	P	graminoid	N/A	npgm
Juncus flavidus	Juncaceae	P	graminoid	N/A	npgm
Juncus subsecundus	Juncaceae	P	graminoid	N/A	npgm
Luzula densiflora	Juncaceae	P	graminoid	N/A	npgm
Mentha saturjioides	Lamiaceae	P	forb	N/A	npfdl
Scutellaria humilis	Lamiaceae	P	forb	N/A	npfdl
Ajuga australis	Lamiaceae	P	forb	N/A	npfdt
Linum marginale	Linaceae	A	forb	N/A	naf
Isotoma axillaris	Lobeliaceae	P	forb	N/A	npfdt
Lomandra filliformis	Lomandraceae	P	moncot forb	N/A	npfm
Lomandra multiflora	Lomandraceae	P	moncot forb	N/A	npfm
Sida corrugata	Malvaceae	P	forb	N/A	npfdl

Species	Family	Life history	Growth form	C pathway	Group
Sida cunninghamii	Malvaceae	P	forb	N/A	npfdl
Eremophila debilis	Myoporaceae	P	forb	N/A	nshrub
Boerhavia dominii	Nyctaginaceae	A	forb	N/A	naf
Epilobium billardierianum	Onagraceae	P	forb	N/A	npfdt
Ophioglossum lusitanicum	Ophioglossaceae	A	fern	N/A	naf
Microtis unifolia	Orchidaceae	P	moncot forb	N/A	npfm
Unknown	Orchidaceae	P	moncot forb	N/A	npfm
Oxalis perennans	Oxalidaceae	P	forb	N/A	npfdl
Dianella spp.	Phormiaceae	P	moncot forb	N/A	npfm
Plantago turrifera	Plantaginaceae	A	forb	N/A	naf
Plantago dubium	Plantaginaceae	P	forb	N/A	npfdl
Eragrostis elongata	Poaceae	A	grass	C4	eag
Eriochloa pseudoachrotricha	Poaceae	A	grass	C4	nag
Danthonia auriculata	Poaceae	P	grass	C3	npgc3
Danthonia caespetosa	Poaceae	P	grass	C3	npgc3
Danthonia linkii	Poaceae	P	grass	C3	npgc3
Danthonia longifolia	Poaceae	P	grass	C3	npgc3
Danthonia monticola	Poaceae	P	grass	C3	npgc3
Danthonia racemosa	Poaceae	P	grass	C3	npgc3
Danthonia setacea	Poaceae	P	grass	C3	npgc3
Dichelachne micrantha	Poaceae	P	grass	C3	npgc3
Elymus scaber	Poaceae	P	grass	C3	npgc3
Microlaena stipoides	Poaceae	P	grass	C3	npgc3
Poa seiberiana	Poaceae	P	grass	C3	npgc3
Stipa bigeniculata	Poaceae	P	grass	C3	npgc3
Stipa densiflora	Poaceae	P	grass	C3	npgc3
Stipa nodosa	Poaceae	P	grass	C3	npgc3
Stipa scabra	Poaceae	P	grass	C3	npgc3
Stipa setacea	Poaceae	P	grass	C3	npgc3
Stipa verticillata	Poaceae	P	grass	C3	npgc3
Aristida behriana	Poaceae	P	grass	C4	npgc4
Aristida benthamii	Poaceae	P	grass	C4	npgc4
Aristida ramosa	Poaceae	P	grass	C4	npgc4
Aristida vagans	Poaceae	P	grass	C4	npgc4
Bothriochloa macra	Poaceae	P	grass	C4	npgc4
Chloris truncata	Poaceae	P	grass	C4	npgc4
Cymbopogon refractus	Poaceae	P	grass	C4	npgc4
Dichanthium serecium	Poaceae	P	grass	C4	npgc4
Digitaria brownii	Poaceae	P	grass	C4	npgc4
Digitaria divaricatissima	Poaceae	P	grass	C4	npgc4
Enneapogon gracilis	Poaceae	P	grass	C4	npgc4
Enneapogon nigricans	Poaceae	P	grass	C4	npgc4
Enteropogon acicularis	Poaceae	P	grass	C4	npgc4
Eragrostis benthamii	Poaceae	P	grass	C4	npgc4
Eragrostis molybdea	Poaceae	P	grass	C4	npgc4
Eragrostis parviflora	Poaceae	P	grass	C4	npgc4
Eulalia aurea	Poaceae	P	grass	C4	npgc4
Panicum effusum	Poaceae	P	grass	C4	npgc4
Paspalidium aversum	Poaceae	P	grass	C4	npgc4

Species	Family	Life history	Growth form	C pathway	Group
Paspalidium constrictum	Poaceae	P	grass	C4	npgc4
Paspalidium distans	Poaceae	P	grass	C4	npgc4
Paspalidium gracilis	Poaceae	P	grass	C4	npgc4
Sporobolus creber	Poaceae	P	grass	C4	npgc4
Tripogon loliformis	Poaceae	P	grass	C4	npgc4
Rumex brownii	Polygonaceae	P	forb	N/A	npfdl
Ranunculus sessiflorus	Ranunculaceae	A	forb	N/A	naf
Clematis glycinoides	Ranunculaceae	P	forb	N/A	npfdl
Aphanes arvensis	Rosaceae	A	forb	N/A	naf
Acaena echinata	Rosaceae	P	forb	N/A	npfdl
Gallium gaudichaudii	Rubiaceae	A	forb	N/A	naf
Gallium propinquum	Rubiaceae	A	forb	N/A	naf
Asperula conferta	Rubiaceae	P	forb	N/A	npfdl
Veronica plebia	Scrophulariaceae	P	forb	N/A	npfdl
Cheilanthes austrotenuifolia	Sinopteridaceae	P	forb	N/A	npfern
Cheilanthes distans	Sinopteridaceae	P	forb	N/A	npfern
Nicotiana suaveolens	Solanaceae	P	forb	N/A	npfdt
Pimelia curviflora	Thymelaeaceae	P	shrub	N/A	nshrub
Pimelia micrantha	Thymelaeaceae	P	shrub	N/A	nshrub
Parietaria debilis	Urticaceae	A	forb	N/A	naf
Urtica incisa	Urticaceae	P	forb	N/A	npfdt

Key to species groups:

Acronym	Species group	Number of species
EAFL	Exotic annual low-growing forb	25
EAFR	Exotic annual rosette-forming forb	10
EAFT	Exotic annual tall or erect forb	42
EAG	Exotic annual grass or graminoid	28
EAL	Exotic annual legume	15
EPF	Exotic perennial forb	15
EPG	Exotic perennial grass or graminoid	6
NAF	Native annual forb	35
NAG	Native annual grass or graminoid	3
NPFDL	Native perennial forb, low-growing dicot	23
NPFDT	Native perennial forb, tall dicot	24
NPFERN	Native perennial fern	2
NPFM	Native perennial forb, monocot	11
NPGM	Native perennial graminoid	11
NPGC4	Native perennial C4 grass	24
NPGC3	Native perennial C3 grass	17
NSHRUB	Native shrub or sub-shrub	11
THIST	Thistle (all exotic)	7

Appendix 2: Species found in surveys of regional remnants within 200 km of the Burrendong experiment. * indicates species found within 25m by 25m survey plots; + indicates species found in other parts of the remnant. Condition classes were formed based on speices composition and expert opinion (S. Prober, K. Thiele, and G. Tonkin).

		Good condition				Intermediate Condition					Poor condition		
Species	origin	Killaloe	Tonkin 1	Camp	Candomine	Camp Cleared	Carroll	Weston	Pinecliffe	Caves	Caves degraded	Tonkin 2	Gate 110
Acaena sp.	native	*	*		+	*		*	*			*	
Aira elegans	exotic	+											
Ajuga australis	native	*											
Alternanthera dentata	native												*
Anagallis arvensis	exotic	+							*				
Arctotheca calendula	exotic											*	
Aristida behriana	native				+								
Aristida ramosa	native	*	*	*	*	*			*	*			*
Aristida vagans	native				+								
Arthopodium minus	native	+			+								
Asperula conferta	native	*	*	*	+	*		*					
Avena sp.	exotic				*		*						
Bothrirochloa macra	native	*		*	*	*	*	*	*	*			*
Brachycome heterodonta	native	*											
Brachyscome spathulata	native				+								
Bracteantha viscosa	native			*					*				
Brassica nigra	exotic												*
Briza minor	exotic	+											
Bromus diandrus	exotic	+											
Bromus hordeaceus	exotic	+											
Bromus madrietensis	exotic				*		*						*
Bromus molliformis	exotic	*		*	*	*	*	*	*	*	*	*	*
Bulbine bulbosa	native	+			+								

		Good condition					Intermediate Condition					Poor condition		
			Tonkin				Camp					Caves	Tonkin	Gate
Species	origin	Killaloe	1	Camp	Candomine		Cleared	Carroll	Weston	Pinecliffe	Caves	degraded	2	110
Calotis lappulacea	native				+									
Carduus tenuiflorus	exotic				+		*						*	*
Carex inversa	native	*	*		+		*			*				
Carthamus lanatus	exotic			*			*	*			*		*	*
Centauria melitensis	exotic			*	*						*	*		*
Centaurium erythraea	exotic	+		*	+		*							*
Chamaecyce drummondii	native		*	*			*						*	
Cheilanthus austrotenuifolia	native	*	*	*	+		*			*				*
Chenopodium desertorum	native				+									
Chenopodium pumilo	native												*	*
Cheilanthes distans	native	+												
Chloris truncata	native				+		*						*	*
Chondrilla juncea	exotic	*	*		*		*		*	*			*	
Chyrsocephalum apiculatum	native	*			+									
Circium vulgare	exotic	*		*	*		*	*		*			*	
Convulvulus erubescens	native		*		*		*				*			
Cymbonotus lawsonianus	native	*	*		*		*		*	*				
Cymbopogon refractus	native	*		*				*		*				
Cynodon dactylon	exotic													*
Cynoglossum suaveolens	native	+			+									
Danthonia caespetosa	native				*									
Danthonia carphoides	native	+												

		Good condition				Intermediate Condition					Poor condition		
			Tonkin			Camp					Caves	Tonkin	Gate
Species	origin	Killaloe	1	Camp	Candomine	Cleared	Carroll	Weston	Pinecliffe	Caves	degraded	2	110
Danthonia eriantha	native				+								
Danthonia linkii	native		*	*									
Danthonia monticola	native				+								
Danthonia racemosa	native	*		*	*	*	*	*	*	*		*	*
Danthonia tenuior	native				+			*		*			
Daucus glochidiatus	native	+			+								
Davesia genistifolia	native	+											
Desmodium varians	native	*	*	*		*		*	*				
Dianella longifolia	native	*		*	+	*			*	*			
Dianella revoluta	native				+								
Dicanthium sericeum	native					*			*	*			
Dichelachne micrantha	native		*	*	+	*							
Dichondra repens	native		*	*	*	*		*	*	*		*	
Dichopogon fimbriatus	native	+			+			*					
Digitaria brownii	native					*			*				
Digitaria divericatissima	native			*									
Diuris punctata	native				+								
Echium plantagineum	exotic	+			*	*					*	*	*
Einedia nutans	native	*	*		*		*	*	*	*		*	
Einedia polygonoides	exotic											*	
Elymus scaber	native	*	*	*	*	*	*	*	*	*			*
Enneapogon gracilis	native			*		*							
Eragrostis parviflora	native												*
Eremophila debilis	native				+								
Erodium cicutarium	exotic												*
Erodium crinitum	native											*	

		Good condition					Intermediate Condition					Poor condition		
Species	origin	Killaloe	Tonkin 1	Camp	Candomine		Camp Cleared	Carroll	Weston	Pinecliffe	Caves	Caves degraded	Tonkin 2	Gate 110
Galium gaudichaudii	native	+												
Geranium molle	exotic	+						*						*
Geranium solanderi	native	*	*	*	+		*	*		*			*	
Glycine clandistina	native	*			*				*	*				
Glycine tabacina	native	*	*	*	+		*			*	*		*	
Gnaphalium sphaericum	native				+									
Gonocarpus tetragynus	native	*												
Goodinia pinnatifida	native		*		*			*	*		*			
Haloragis heterophylla	native	+												
Hardenbergia violacea	native	*												
Heliotropium amplexicaule	exotic													*
Heloitropium europaeum	exotic													*
Hibbertia riparia	native	+												
Hordeum leporinum	exotic												*	
Hydrocotyle laxiflora	native	*	*		+		*		*	*	*			
Hypericum gramineum	native	*		*	+		*							
Hypericum perforatum	exotic			*	+		*		*	*	*			*
Hypochaeris glabra	exotic	+												
Hypochaeris radicata	exotic	*	*				*	*	*	*	*		*	
Indigophora adesmiifolia	native	*								*				
Juncus subsecundus	native						*			*				
Juncus usitatus	native		*		+									

		Good condition					Intermediate Condition					Poor condition		
			Tonkin				Camp					Caves	Tonkin	Gate
Species	origin	Killaloe	1	Camp	Candomine		Cleared	Carroll	Weston	Pinecliffe	Caves	degraded	2	110
Lactuca saligna	exotic						*							
Lepidium pseudohyssopifolium	native									*				*
Leptorhynchus squamatus	native	*			+									
Linum marginale	native	+					*							
Linum trigynum	exotic			*										
Lissanthe strigosa	native	*												
Lolium sp.	exotic	*			*			*		*				
Lomandra filiformis	native	+			*				*	*				
Lomandra longifolia	native				*									
lomandra multiflora	native	*	*	*	*		*			*				
Luzula sp.	native	+			+									
Maireana microphylla	native				+									*
Malva parviflora	exotic												*	*
Marrubium vulgare	exotic				*									*
Medicago arabica	exotic							*					*	
Medicago minima	exotic	+									*			
Microlaena stipoides	native				+			*		*	*			
Microtis unifolia	native		*	*										
Modiola caroliniana	exotic												*	*
Opuntia stricta	exotic			*			*							
Orobanche minor	exotic	*	*		+					*				
Oxalis corniculata	exotic			*			*			*	*		*	*
Oxalis perennans	native	*	*		*			*	*					
Panicum effusum	native		*	*	+		*	*		*	*			
Paronycha brasiliana	exotic							*						
Paspalidium aversum	native													*

		Good condition				Intermediate Condition					Poor condition		
		Tonkin				Camp					Caves	Tonkin	Gate
Species	origin	Killaloe	1	Camp	Candomine	Cleared	Carroll	Weston	Pinecliffe	Caves	degraded	2	110
Paspalidium distans	native				*								
Paspalum dilatum	exotic				+				*				
Petroraghia nanteulii	exotic	*	*	*	*		*		*				
Phalaris tuberosa	exotic		*		+							*	
Pimelia curviflora	native	*	*				*						
Pimelia glauca	native	*											
Plantago turrifera	exotic									*			
Plantago varia	native	+	*		*				*				
Plolygonum arenastrum	exotic												*
Poa sieberiana	native	*	*	*	*	*	*		*				
Polygala japonica	native	+											
Portulaca oleracea	exotic												*
Pterostylis sp.	native	+			+								
Rubus fruticosus	exotic	*											
Rumex brownii	native	*		*	*	*	*	*	*	*		*	*
Salvia verbinacea	exotic	*			*	*		*		*		*	
Schoenus apogon	native	+											
Senecio quadridentatus	native	+		*		*							
Senna barclayana	native												*
Sida corrugata	native			*	+					*		*	*
silene nocterna	exotic				*								
Silybum marianum	exotic				+		*				*	*	*
Sisymbrium sp.	exotic									*			
Solanum cinereum	exotic			*									
Solanum nigrum	exotic						*						*
Solenogyne dominii	native	+						*	*				
Sonchus oleraceus	exotic				+			*	*				

		Good condition				Intermediate Condition					Poor condition		
Species	origin	Killaloe	Tonkin 1	Camp	Candomine	Camp Cleared	Carroll	Weston	Pinecliffe	Caves	Caves degraded	Tonkin 2	Gate 110
Sporobolus creber	native				+	*	*						
Stackhousia monogyna	native	+			+	*							
Stellaria media	exotic		*					*					
Stipa bigeniculata	native				*		*	*					
Stipa densiflora	native			*				*					
Stipa scabra	native		*	*	*	*	*		*	*			*
Stipa verticillata	native				+								*
Swainsona oroboides	native	+											
Templetonia stenophylla	native	+											
Themeda australis	native	*		*	+	*							
Trifolium angustifolium	exotic	*	*	*	*	*		*	*				
Trifolium arvense	exotic	+		*			*	*					
Trifolium scabrum	exotic			*									
Trifolium subterraneum	exotic	*	*				*		*			*	
Tryptilodiscus pygmaeus	native	+			+								
Urtica urens	exotic											*	
Verbascum virgatum	exotic				+	*							
Verbena bonariensis	exotic												*
Vittadinia cuneata	native	+		*		*		*					
Vittadinia muelleri	native	+											
Vittadinia pustulata	native				*								
Vulpia sp.	exotic	+					*	*				*	
Wahlenbergia communis	native			*		*	*						
Wahlenbergia luteola	native	*	*		*		*	*	*	*			

		Good condition				Intermediate Condition					Poor condition		
Species	origin	Killaloe	Tonkin 1	Camp	Candomine	Camp Cleared	Carroll	Weston	Pinecliffe	Caves	Caves degraded	Tonkin 2	Gate 110
Wahlenbergia stricta	exotic	*	*						*	*			
Wurmbia dioica	native	+			+								
Xanthium spinosum	exotic					*							*
Eulalia aurea	native								*				
Briza maxima	exotic								*				
Scutellaria humilis	native								*				
conyza canadensis	exotic								*				

Appendix 3: Summary of the Landscape Function Analysis technique for assessing rangeland condition (reproduced with permission from D. Tongway and N. Hindley, and available at www.cse.csiro.au/research/program2/Resources/LFA_Summary.pdf)

LANDSCAPE FUNCTION ANALYSIS: A SYSTEMS APPROACH TO ASSESSING RANGELAND CONDITION

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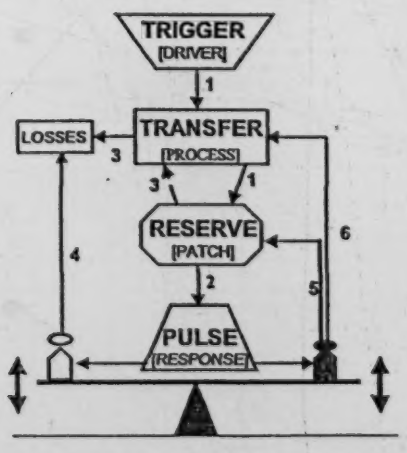
ABSTRACT

We propose a procedure for the assessment of rangeland function, comprised of three components: a conceptual framework, a field methodology and an interpretive framework. The conceptual framework treats landscapes as systems: defining how landscapes work in terms of sequences of processes regulating the availability of scarce resources. The field methodology uses indicators at landscape and patch scale to provide and structure information to satisfy the needs of the conceptual framework. The interpretational framework provides a process to identify critical thresholds in landscape function and thus provide a function-based state and transition landscape assessment. The approach is quick and simple in the field, is applicable to all range landscapes and amenable for use by a wide range of end-users.

INTRODUCTION

Rangeland monitoring has typically been descriptive: restricted to evidence provided by a narrow range of biota or associated with theories of plant succession (Golley 1977). Methods have also been largely tied to pastoralism as the only land-use. This situation is now changing, with a broader societal use of rangelands. Monitoring and comparing landscapes on an inter-regional and national basis, for example the National Land and Water Audit, would be facilitated if the procedures were widely applicable and the data directly comparable. Walker (1996) called for an understanding of how rangelands function by building conceptual models. Ludwig and Tongway (1997) presented a systems-based framework (trigger-transfer-reserve-pulse — TTRP, Figure 1) for the way in which rangelands function, based on how landscapes function to conserve and utilise scarce resources. This framework also facilitated the development of more detailed simulation models (e.g. Ludwig and Marsden 1995), enabling the role of these models to be seen in a wider, landscape context.



Ref	Processes Involved	
1	• Run-on • Storage/Capture	• Deposition • Saltation capture
2	• Plant germination, growth • Nutrient mineralisation	• Uptake processes
3	• Run-off into streams • Rill flow and erosion	• Shoot erosion out of system • Wind erosion out of system
4	• Herbivory • Fire	• Harvesting • Deep drainage
5	• Seed pool replenishment • Organic matter cycling/Decomposition processes • Harvest/Concentration by soil micro-fauna	
6	• Physical obstruction/Absorption processes	

Figure 1. The TTRP framework representing sequences of ecosystem processes and feedback loops. The table lists some of the processes operating at different locations in the framework.

METHOD DEVELOPMENT

The TTRP framework represents a sequence of landscape processes and feedback loops in an inclusive manner, enabling the structuring of environmental information. Methods to assess soil productive potential linked to plant performance had been developed to a certain stage (Tongway and Smith 1989, Ludwig and Tongway 1992), but needed the spatial and inter-regional context to become more useful to potential stakeholders. The soil condition indicators were initially developed from geomorphic processes such as erosion, crust formation, litter decomposition and correlates observed in the field. The validity of these indicators was enhanced by laboratory experiments (Mücher *et al.* 1988, Greene *et al.* 1994) and field measurements (Tongway 1993, Greene 1992). Spatial analysis of a number of landscape types (Ludwig and Tongway 1995) suggested a means by which the soil indicators could be packaged for use in different landscape types.

In 1992-1995, NSCP funding brokered by Ag WA facilitated the development of extensively applicable methods, integrating soil surface condition procedures with the emerging TTRP framework. This resulted in a nested hierarchical information system. The method was overtly linked to land system resource map bases (e.g. Mitchell *et al.* 1988; many others). Land units as sub-units within land systems were recognised, with the monitoring site located within the land unit. Australian standard methods (McDonald *et al.* 1990) were used to provide landform and slope characterisation.

THE METHOD IN OPERATION

"Landscape organisation" is the coarsest form of LFA data and is the first step in data collection. Data are collected on a line transect oriented in the direction of resource flow (usually down slope, but aeolian landscapes would use wind direction). Landscape features that interrupt, divert or absorb runnoff and transported materials are recorded according to protocols outlined in the technical methods manual (Tongway 1994, Tongway and Hindley 1995, 2000). Typically, zones of resource loss (source or runoff zones) are distinguished from zones of resource gain (sink or runon zones) and their relative sizes measured. Several indices of landscape organisation can be deduced from these data. In addition, the data provides a "map" of the transect. In the second step, each zone type, 10 soil surface variables, plus soil texture are assessed, using the methods in the manuals. These observations are both simple and quick after a little practice. Vegetation parameters (such as density, species composition, size) can also be collected from the same transect by plotless, distance measuring techniques (Bonham 1979), as well as indicators of habitat complexity for mammals and birds (Newsome and Catling 1979).

CALCULATION OF INDICES

The soil surface data are combined in different combinations to reflect three major soil habitat quality indices: stability or resistance to erosion, infiltration/water holding capacity and nutrient cycling (Figure 2). The data are presented in percentage terms.

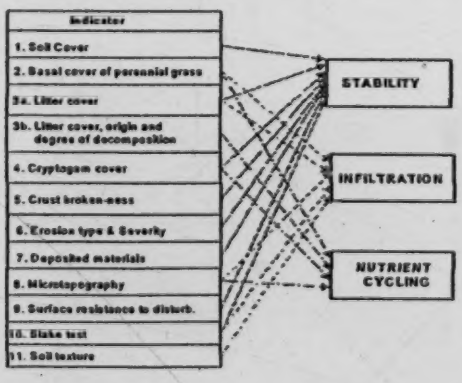


Figure 2.
The combination of Soil Condition Classes to derive indices of Stability, Infiltration and Nutrient Cycling.

INTERPRETATIONAL FRAMEWORK

The tabulated values need to be interpreted in the landscape context to make the most use of their information potential. With extensive experience, one might be able to place useful interpretations on each of the index values, but this is a haphazard process. The most recent development in LFA is the process whereby a response surface in the form of a sigmoidal curve is generated from field data (Tongway and Hindley 2000). The curve relates functional status with stress and disturbance. To fit this curve, one needs data from both extremes of the available data space as well as "typical" sites encountered in monitoring which will have intermediate values. The response surface (Figure 3) recognizes the upper asymptote as the biogeochemical potential of the site limited by climate and parent material and the lower asymptote as the lower limit of function under the existing land use stress. The slope of the line joining the asymptotes reflects the "robustness" or "fragility" of the system.

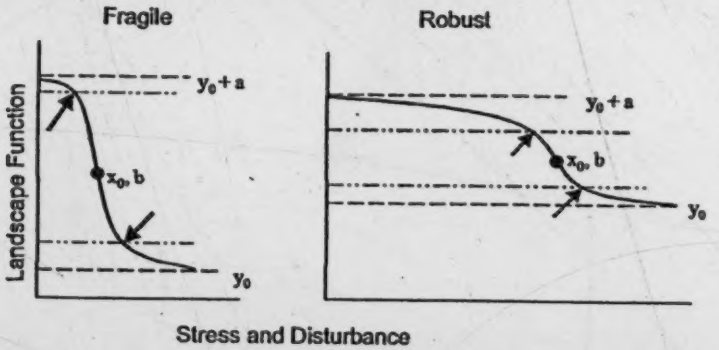


Figure 3. Examples of response curves for fragile and robust landscapes. The initial response of landscape function to stress and/or disturbance is markedly different. The fragile landscape deteriorates with low stress and has a much lower base line y_0 then the more robust landscape. Four-parameter sigmoid curves of the form

$$y = (y_0 + a) / 1 + e^{-(x-x_0)b}$$

provide four practical values reflecting the nature of the landscape. Critical thresholds (arrows) for each of the indices can be determined from field data.

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